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A RECLASSIFICATION OF THE GENERA OF THE CLICK BEETLE TRIBE ELATERINI, BASED ON THE RECONSTRUCTED PHYLOGENY

(COLEOPTERA: ELATERIDAE)

BY

EDWARD R. FULLER ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

DEPARTMENT OF ENTOMOLOGY

Edmonton, Alberta

Fall, 1994

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "A Reclassification of the Genera of the Click Beetle Tribe Elaterini, Based on the Reconstructed Phylogeny (Coleoptera: Elateridae)" by Edward R. Fuller in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dr. Dale Vitt

Dr. Daniel K. Young

Dr. Ron Gooding

12 May 1994

ABSTRACT

The click beetle tribe Elaterini (sensu novo) is redefined based on previously unrecognized synapomorphic character states of the adult gena and mandible. The type genera of the traditional tribes Elaterini, Pomachiliini, Adrastini and Agriotini are included in this monophyletic group. The Pomachiliini, Adrastini and Agriotini are shown to consist of relatively derived taxa of the Elaterini and the former three tribes are combined with the Elaterini and the names synonymized. Of the 90 genera assigned to one of the four traditional tribes, 35 are retained in the Elaterini (sensu novo): Adrastus Eschscholtz, Agelasinus Candèze, Agriotella Brown, Agriotes Eschscholtz (including subgenus Ectinus Eschscholtz), Aphanobius Eschscholtz, Atractopterus LeConte, Betarmon Kiesenwetter, Chatanayus Fleutiaux, Cosmesus Eschscholtz, Ctenoplus Candèze, Dalopius Eschscholtz, Deromecus Solier, Diplostethus Schwarz, Elater Linnaeus, Glyphonyx Candèze, Insuliectinus Kishii, Leptoschema Horn, Medonia Candèze, Mesembria Arnett, Neotrichophorus Jacobson, Orthostethus Lacordaire, Panspoeus Sharp, Paracosmesus Schwarz, Parallelostethus Schwarz, Parasilesis Ohira, Peripontius Guryeva, Pittonotus Kiesenwetter, Pomachilius Eschscholtz, Probothrium Candèze, Pseudagriotes Schwarz, Pseudoderomecus Fleutiaux, Silesis Candèze, Smilicerus Candèze, Synaptus Eschscholtz and Ypsilostethus Candèze. These genera have not been shown to be monophyletic. Preliminary diagnoses are presented for these genera, and a detailed discussion of character states in the tribe is provided.

Seven genera are placed in the outgroup of the Elaterini, the tribe Sericosomini: Sericus Eschscholtz, Agonischius Candèze, Sadoganus Ohira, Chiagosnius Fleutiaux, and tentatively, Dolerosomus Motschulsky, Ectinoides Kishii and Vuilletus Fleutiaux. An autapomorphic character state for the Sericosomini has not been identified, and the monophyly of this tribe is unproven.

Affinities and possible affinities of 33 of the remaining 48 genera are discussed briefly. The status of the other 15 genera is unknown since specimens were unavailable for study.

An hypothesis of reconstructed phylogeny is presented for the Elaterini (sensu novo) based on 37 characters and 32 taxa. The significance of some character states, especially those involved in the "jump" mechanism of click beetles, is discussed. Biogeographical implications of the reconstructed phylogeny also are discussed.

ACKNOWLEDGEMENTS

This study could not have been completed without the seemingly endless support and patience of both my supervisor, G.E. Ball, and my wife, Janet Webb.

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TABLE OF CONTENTS

Introduction 1
Material and Methods 6
    Material 6
        Taxa Included in the Elaterini 6
        The Outgroup of the Elaterini 7
    Methods 7
        Taxonomic Rankings 7
        Treatment of Specimens 9
Structural Features of Elaterini 11
    Generic Groups of Convenience 11
    General Characteristics of Elaterini 11
    Head Capsule and Appendages 12
        Gena 12
        Supraantennal crests/Frontal carina .. 12
        Periocular space 13
        Antennae 14
        Eyes 14
        Labrum/Epipharynx 14
        Mandibles 15
        Maxillae 18
        Labium 19
    Prothorax 19
        Anterior subpronotal lobe 20
        Lateral carina 20
        Hind angles 20
        Mesal margin of hypomeron 21
        Pronotosternal sutures 22
        Prosternum 22
        Prosternal mucro 22
        Proendosternite 23
    Mesothorax 23
        Mesosternum 24
        Mesepimeron 26
    Metathorax 26
        Metasternum 27
        Median groove 27
        Lateral groove 27
    Legs 27
        Mesotrochantin 28
        Metacoxal plate 28
        Tarsomeres 28
        Tarsal claws 29
    Abdomen 29
        Male Genitalia 29
        Female Genitalia 30
          Abdominal segment VIII 30
          Spiracular sclerite of segment VIII 30
          Ovipositor 31
          Vagina 32
          Bursa copulatrix 32
          Armature of bursa copulatrix 34

Accessory glands 35
Colleterial glands 36
Classification of Elaterini 37
Tribe Elaterini Leach 37
Key to Genera of Elaterini 38
Genus Aphanobius Eschscholtz 43
Genus Neotrichophorus Jakobson 44
Genus Pittonotus Kiesenwetter 45
Genus Diplostethus Schwarz 46
Genus Atractopterus LeConte 47
Genus Leptoschema Horn 48
Genus Orthostethus Lacordaire 49
Genus Elater Linnaeus 49
Genus Parallelostethus Schwarz 52
Genus Probothrium Candèze 53
Genus Agelasinus Candèze 54
Genus Ypsilostethus Candèze 55
Genus Mesembria Arnett 56
Genus Dalopius Eschscholtz 57
Genus Agriotes Eschscholtz 59
Genus Agriotella Brown 63
Genus Cosmesus Eschscholtz 64
Genus Deromecus Solier 64
Genus Medonia Candèze 65
Genus Pseudoderomecus Fleutiaux 66
Genus Betarmon Kiesenwetter 66
Genus Paracosmesus Schwarz 67
Genus Pomachilius Eschscholtz 68
Genus Adrastus Eschscholtz 69
Genus Synaptus Eschscholtz 70
Genus Parasilesis Ohira 71
Genus Ctenoplus Candèze 72
Genus Peripontius Guryeva 73
Genus Glyphonyx Candèze 74
Genus Silesis Candèze 76
Genus Chatanayus Fleutiaux 77
Genus Insuliectinus Kishii 78
Genus Panspoeus Sharp 78
Genus Pseudagriotes Schwarz 79
Genus Smilicerus Candèze 80
Genera Excluded From Elaterini 82
Taxa of Unknown Status 94
Evolutionary Considerations 97
Taxa Studied 97
Monophyly of the Elaterini + Sericosomini . 97
Monophyly of the Elaterini 97
Phylogenetic Designation of Character States 98
Calculation of Reconstructed Phylogeny ... 104
Reconstructed Character Evolution 105
Biogeographical Considerations 112
Concluding Remarks 114
Literature Cited 115

LIST OF TABLES

Table 1: Summary of possible affinities of taxa excluded from Elaterini and Sericosomini . 131-132
Table 2. Distribution of phylogenetically designated character states among taxa of the tribe Elaterini. 133-135
Table 3. Summary of Character State Changes in Figs. 12-19 136-138

LIST OF FIGURES

Figure 1. Scanning electron micrographs of head structures 140
Figure 2. Photographs of epipharynx 142
Figure 3. Scanning electron micrographs of mandibles 144
Figure 4. Scanning electron micrographs of mandibles, maxilla and pronota 146
Figure 5. Scanning electron micrographs of prothorax 148
Figure 6. Scanning electron micrographs of prosternal mucro 150
Figure 7. Scanning electron micrographs of prothorax, mesosternum 152
Figure 8. Scanning electron micrographs of ventral mesothoracic structures 154
Figure 9. Scanning electron micrographs of meso- and metathoracic structures 156
Figure 10. Scanning electron micrographs of tarsi, photographs of female genital structures 158
Figure 11. Photographs of bursa copulatrices . 160
Figure 12. Hypothesized reconstructed phylogeny of the Elaterini 162
Figures 13-15. Possible resolutions of polychotomies in Fig. 12 164
Figures 16-19. Possible resolutions of polychotomies in Fig. 12 166
Figure 20. Hypothesized reconstruction of land mass configurations in Late Cretaceous, showing probable dispersal route of Ancestor H 168
Figure 21. Hypothesized reconstruction of land mass configurations in Paleocene, showing probable dispersal route of Ancestors N and R, or Ancestor MC 170

INTRODUCTION

> "Nearly everyone who has worked on the elaterids has become frustrated sooner or later (more often sooner!) because there are so many problems at the generic level and proportionally the same number at the tribal or subfamilial level." (Becker, 1979:401).

It has become something of a tradition in Elateridology to begin taxonomic treatises with a complaint about the horrible state of elaterid classification (Calder, 1986). For my contribution, I paraphrase Darwin in reference to Becker's quote above: Frustration is a weak term to express the feelings of a taxonomist who for the first time has wandered by himself in elaterid classification.

The Elateridae are a family of beetles colloquially referred to as "click beetles", "snapping beetles" and "skip jacks" among others (Hyslop, 1915). These names refer to the ability of adults to "click" or "snap" the prothorax against the mesothorax when flipped on their backs or held between fingers. This characteristic is generally regarded as being unique to the Elateridae, though some species of the related family Eucnemidae also "click" effectively (personal observation). With at least 7,000 described species (Schenkling, 1925, 1927), the Elateridae are moderately speciose. Representatives are found on every continent except Antarctica, with the greatest number of species living in tropical and subtropical regions.

Larvae are called wireworms, apparently in reference to the hard cuticle and slenderness of some species of Agriotes Eschscholtz (Hawkins, 1936). Larvae of a few species are important pests of cultivated plants (Hyslop, 1915; Hawkins, 1936; Arnett, 1962).

Adults, as a group, range in size from about 2mm up to 60mm in length, with most species 5-15mm. Adults of some species are strikingly coloured, but most are various shades of dull brown. In habitus, adults of most species are remarkably homogeneous in appearance, a characteristic that has contributed to the difficulties of elaterid classification and identification. However, elaterids themselves did not propose the classification of the family or the characters used for their identification, and it has been the actions of elateridologists that has resulted in the state of confusion and frustration to which many workers have alluded.

Miss Christine von Hayek, formerly of the Natural

History Museum, London [the former British Museum (Natural History)], undoubtably has more experience than anyone in dealing with the difficulties of elaterid classification, through her careful studies of the Agrypninae (Hayek, 1973, 1979) and the Melanotus group (Hayek, 1990). I consider her opinions and judgment invaluable, and she has explained more lucidly than anyone else the reasons behind the present state of elaterid classification. For these reasons, I quote her at length.

In her opinion, the principal deficiency of past elateridologists has been their regional, rather than global, perspective:

> "... workers have restricted their studies to artificially circumscribed areas (countries or states) or to one geographical region. By doing so, they have remained unaware that many of the classic character states, traditionally regarded as of prime importance at generic rank, are not constant and frequently merge imperceptibly into one another, and also that the various states of different characters appear in a much larger range of combinations than they thought." (Hayek, 1990:38-39)

Even considering the regional nature of most publications, much of the work itself is of limited usefulness. I have been continually frustrated by my inability to confidently identify specimens using published information because of a great reliance on relative character states (e.g., 'pronotal punctures less dense' or 'body more slender') for diagnoses, and the fact that almost none of these diagnostic character states are illustrated. Apparently I have not been alone:

> "The difficulty of interpreting many descriptions has also contributed to the confusion. Because accurate unambiguous diagnoses of taxa are difficult to produce, many descriptions take the form of comparisons with previously described taxa or the author's interpretation of them. As every worker's interpretation of a character or taxon is subjective, strongly influenced by his or her knowledge and experience of the group, and by the appearance of the last specimen examined, these descriptions are often very misleading and the majority are more noteworthy for the information which is omitted than for that which is included." (Hayek, 1990:39)

Hayek (1990:39) concludes:

> "Experience has shown that it is not safe to

> assume that because a species is attributed to a particular genus it necessarily possesses the diagnostic features of that genus. Furthermore, little or no effort has been made to discover new characters and evaluate the states in which they appear. Where a new character (or more accurately, character state) has been found its discoverer has rarely, if ever, considered it necessary to examine other species for its presence before employing it as the diagnostic feature of a new taxon of generic or even higher rank. On other occasions the diagnoses of extant genera have been modified to include the newly discovered character state without first ascertaining whether the type species possesses the feature in question. Not surprisingly these activities have led to the establishment of what can best be described as a series of interlocking taxa at both the genus- and family-group rank."

Hayek's comments should be kept in mind when reading any paper on elaterids, including this one.

This study began as a search for characters that would support the monophyly of Dalopius Eschscholtz. I noticed in Dalopius an apparently unique configuration of the gena around the mandibular condyles. While this configuration quickly proved to be a dismal failure as an apomorphy for Dalopius, it did identify a monophyletic group that included Elater Linnaeus, Agriotes Eschscholtz, Adrastus Eschscholtz, and Pomachilius Eschscholtz, the type genera of the tribes Elaterini, Agriotini, Adrastini and Pomachiliini.

The traditional classification of these tribes was proposed by Candèze (1860, 1863). While his classification has remained virtually unchanged (except for the addition of newly described genera), it has done so as a result of inertia rather than from stability based on a fundamentally sound classification.

Candèze (1860) placed six genera in the 'Pomachiliites', and although diagnostic character states were proposed, he conceded the tribe was based more on habitus than character states; his 'Pomachiliites' had relatively long, narrow bodies. Nineteen genera were included in the 'Ludiites' (Candèze, 1863) (=Elaterini) based principally on the convex frons and oblique supraantennal crests. He also recognized two subgroups based on whether or not the metacoxal plate was toothed. Those genera related to Ludius Berthold (= Elater) had toothed metacoxal plates; those related to Agriotes did not. The 'Adrastites' included five genera which had

pectinate tarsal claws but otherwise were little different from the Agriotes subgroup of 'Ludiites' (Candèze, 1863).

From the arrangement of tribes, Candèze (1860) considered the 'Pomachiliites' to be more closely related to the 'Physorhinites' and 'Cryptohypnites' than to the 'Ludiites' (=Elaterini) and 'Adrastites'. Candèze (1891) largely followed his previous classifications, though the subgroups of 'Ludiites' were not recognized; he included 12 genera in 'Pomachiliites', 28 genera in 'Ludiites' and the five genera in 'Adrastites'. Champion (1894-1896), in the Biologia Centrali-Americana, largely followed the classification of Candèze (1891), but recognized a tribe for genera related to Agriotes and used the modern suffix '-ini' for the tribal names. The family group name Agriotini is traditionally credited to Champion (1895), though a family group name based on Agriotes, Agriotites, was used by Castelnau (1840). Aside from adding genera described after 1891, Schwarz (1906-7) also followed the classification and implied relationships of Candèze (1891); the Pomachiliini had grown to include 16 genera, the Steatoderini (= Elaterini) included 41 genera, and the Adrastini remained at five included genera. The last world catalogue of Elateridae, Schenkling (1925, 1927) in the Coleoptorum Catalogus, largely followed the classification of Schwarz (1906-7), but all tribes were treated as subfamilies. The number of genera included in the Pomachiliinae was 18, that of Ludiinae, 39, and that of Synaptinae (= Adrastini), five. Two genera of relevance to this study, Leptoschema Horn and Ypsilostethus Candèze, were placed in the Athoinae and Megapenthini, respectively. Subsequent cataloguers have followed Schenkling (1925, 1927).

The close relationship between the Pomachiliini, Agriotini and Adrastini was recognized by Guryeva (1974, 1979b). However, in 1974, Guryeva's treatment of the Pomachiliini was inconsistent; she included Pomachilius in the Agriotini, but mentioned the Pomachiliini and Agriotini in the diagnosis of the subfamily Elaterinae. In 1979, she treated the Agriotini and Adrastini as subtribes of Pomachiliini. However, her study dealt only with Palaearctic genera and the included taxa were largely those included by Schenkling (1925, 1927) in these tribes.

I have now identified 90 genera that have been placed explicitly or by implication in one of the Pomachiliini, Elaterini, Adrastini or Agriotini, three times the number included in these tribes when they were proposed more than 130 years ago. No attempt has ever been made to ascertain whether or not these genera form a monophyletic group.

Studies of the scope and detail applied in this study are relatively rare in the Elateridae. Notable exceptions are the revision of the Crepidomeninae by Calder (1976, 1978, 1981, 1986) and the revision of the Neotropical Hemirhipini by Casari-Chen (1984). The works of both these authors have set an inspiring example.

In this study I have redefined the Elaterini to include only those genera that belong to the monophyletic group that includes Elater, Agriotes, Adrastus and Pomachilius. I have attempted to find new characters on which to base the classification of the Elaterini (sensu novo), and have examined representatives of as many of the genera traditionally assigned to the Elaterini and Pomachiliini sensu Guryeva (1979b) as possible. I believe I am proposing a classification of the Elaterini that will be stable rather than inert.

MATERIAL AND METHODS

MATERIAL

This study is based on examination of 1661 specimens belonging to species placed in the four traditional tribes that make up the Elaterini (sensu novo). At least three times as many specimens of species in other family-group taxa of Elateridae were examined for the presence of the unique configuration of the gena mentioned in the Introduction.

A study of this type would not have been possible without the cooperation of a number of institutions and individuals. Specimens examined were borrowed from or deposited in the collections of the institutions or persons listed below. Names of curators are in parentheses.

BCPM - Royal British Columbia Museum, Victoria, BC (J.A. Cosgrove)
BMNH - The Natural History Museum, London, England (C.M.F. von Hayek, E. DeBoise)
BPBM - Bernice P. Bishop Museum, Honolulu, HI (G.A. Samuelson)
BYUC - Monte L. Bean Life Science Museum, Brigham Young Univ., Provo, UT (R.W. Baumann)
CASC - California Academy of Sciences, San Francisco, CA (D.H. Kavanaugh)
CNCI - Canadian National Collection of Insects, CLBBR, Agriculture Canada, Ottawa, ON (Y. Bousquet)
DEI - Deutsches Entomologische Institut, Eberswalde-Finow, Germany (L. Zerche)
ERFC - collection of the author
IRSNB - Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (K. Desender)
LACM - Natural History Museum of Los Angeles County, Los Angeles, CA (B.V. Brown)
NFRC - Northern Forestry Research Center, Forestry Canada, Edmonton, AB (D.L. Langor)
PMAC - Provincial Museum of Alberta, Edmonton, AB (A.T. Finnamore)
TKC - collection of Dr. Takashi Kishii, Kyoto, Japan
UASM - Strickland Museum, Department of Entomology, University of Alberta, AB (G.E. Ball)
UKSM - Snow Museum, University of Kansas, Lawrence, KS (J.S. Ashe)
USNM - National Museum of Natural History, Smithsonian Institution, Washington, DC (the late D.R. Whitehead, R.D. Gordon)

Taxa Included in the Elaterini

The Elaterini as defined here differs from the traditional definitions of the tribe available in the

literature. For purposes of clarity, I include the following genera in the Elaterini (sensu novo):

Adrastus Eschscholtz
Agelasinus Candèze
Agriotella Brown
Agriotes Eschscholtz
 subgenus Ectinus Eschscholtz
Aphanobius Eschscholtz
Atractopterus LeConte
Betarmon Kiesenwetter
Chatanayus Fleutiaux
Cosmesus Eschscholtz
Ctenoplus Candèze
Dalopius Eschscholtz
Deromecus Solier
Diplostethus Schwarz
Elater Linnaeus
Glyphonyx Candèze
Insuliectinus Kishii
Leptoschema Horn
Medonia Candèze
Mesembria Arnett
Neotrichophorus Jakobson
Orthostethus Lacordaire
Panspoeus Sharp
Paracosmesus Schwarz
Parallelostethus Schwarz
Parasilesis Ohira
Peripontius Guryeva
Pittonotus Kiesenwetter
Pomachilius Eschscholtz
Probothrium Candèze
Pseudagriotes Schwarz
Pseudoderomecus Fleutiaux
Silesis Candèze
Smilicerus Candèze
Synaptus Eschscholtz
Ypsilostethus Candèze

The Outgroup of the Elaterini

The tribe Sericosomini is here designated as the outgroup of the Elaterini. For a discussion of the Sericosomini, see 'Genera Excluded from Elaterini'.

METHODS

This study is based on structural features of adults only. Larvae have been identified for only 11 of the 35 genera I include in the Elaterini, a number I consider insufficient for analysis.

Taxonomic Rankings

The taxonomic ranks applied to the subfamilies, tribes and genera in this study reflect published information, and thus are merely traditional. Ranks of genera described before 1927 are those applied by Schenkling (1925, 1927) unless changed by subsequent workers. Ranks of genera described after Schenkling (1925, 1927) are those applied by the author of the genus, unless changed by subsequent workers. For subfamilies and most tribes, I follow the classification of Stibick (1979). For the traditional ranks of the Pomachiliini, Agriotini and Adrastini, I follow both Stibick (1979), who recognized these as separate tribes, and Guryeva (1979b) who treated the Agriotini and Adrastini as subtribes of the Pomachiliini. Whether I follow Stibick (1979) or Guryeva (1979b) in a given situation depends on context.

At present, I chose to treat the Elaterini (sensu novo) as a tribe within the Elaterinae. This, too, is

merely traditional. I have no evidence the Elaterinae are a monophyletic group, nor do I have any evidence the five other tribes included by Stibick (1979) in the Elaterinae (Dicrepidiini, Odontonychini, Ampedini, Megapenthini and Physorhinini) are, by themselves or collectively, monophyletic. Thus, the relationship of the Elaterini (*sensu novo*) + Sericosomini (the proposed outgroup) to other taxa of Elaterinae is unknown. In the interests of nomenclatural stability, I believe it is inappropriate to institute changes in classification without thorough study. Accordingly, I adopt the published classification and taxonomic ranks for those taxonomic groups I have not studied.

Treatment of Specimens

Techniques used in this study are described in some detail because they differ somewhat from the standard techniques for work with Elateridae (Becker, 1956) and thus have not been used in other studies on the Elateridae.

Unsclerotized tissue was dissolved ("cleared") from whole bodies in a hot (boiling-water bath temperature) or cold (room temperature) solution of 10% potassium hydroxide (KOH). If only the female genitalia needed to be examined, the abdomen was disarticulated from the metathorax and cleared as above. Internally, only tracheal trunks and, in females, reproductive structures of non-mesodermal origin (Becker, 1956) survive clearing by KOH. The length of time required to dissolve soft tissue varies depending on the size of the specimen and original preservative used. Specimens originally preserved in alcohol tend to require more time than those pinned and dried. (Specimens preserved in a formalin-based preservative clear only with extreme difficulty.) Total required time varied from 15-30 minutes in hot KOH to overnight in cold KOH.

The prothorax was disarticulated from the mesothorax and the abdomen was disarticulated from the metathorax. Dissolved tissue was removed from the body cavity with a jet of water from an hypodermic syringe. Remaining tracheal trunks were removed manually. Cleared structures were placed in 5% acetic acid (commercial vinegar) for 5-10 minutes to neutralize the KOH, rinsed in water and preserved in 70% ethanol. Labrum, mandibles, maxillae and mentum were disarticulated from the head capsule and submerged in glycerine for examination. The head capsule including the cervical sclerites were disarticulated from the prothorax and stored with the thorax and abdomen in 70% ethanol.

To remove the female organs of reproduction from the cleared abdomen, segment VIII and genital structures

attached to it were separated from the abdomen by tearing the membrane between segments VII and VIII, and gently pulling segment VIII out the anterior end of the abdominal cavity. The bursa copulatrix inflates in KOH, and some are damaged by being forced through the posterior end of the abdominal cavity. If the abdomen was removed from an uncleared pinned specimen, the cleared abdomen was then glued into its normal position against the metacoxae with shellac glue. For examination, genital structures were placed in a dilute ethanol/glycerine solution (3-4 drops of glycerine mixed with 10-15 ml 70% ethanol), and the ethanol was allowed to evaporate. This usually prevented the bursa from collapsing as would happen if it was placed directly into glycerine. For photography, genital structures were stained for one minute in a 1% solution of Chlorazol Black E in 95% ethanol (Tschinkel & Doyen, 1980). This stain preferentially stains the bursa and its diverticula in elaterids, but for reasons unknown to me, does not appear to stain the colleterial glands or the spermathecal duct. Genital structures were then returned to glycerine using the methods described above.

Because of the paucity of specimens for most species, few specimens were disarticulated (one specimen for most species). To compensate for the small sample sizes, I have chosen characters which present identical or nearly identical configurations in two or more genera. I have assumed that character states which are the same in different genera are the same within those genera and within the species studied. Characters visible without disarticulation were examined on all available specimens; these characters did not provide just cause to question the above assumption. I had sufficient material to disarticulate three to five specimens of Agriotes (sensu stricto) sputator (Linnaeus), Agriotes (Ectinus) aterrimus (Linnaeus), Agriotes fucosus LeConte, Dalopius marginatus (Linnaeus), Neotrichophorus carolinensis (Schaeffer) and Synaptus filiformis (Fabricius). I saw no evidence in these species that the characters I had chosen violated the assumption I made above. Species disarticulated are indicated by an asterisk (*) under Material Examined of each genus in the Classification section.

All structures were examined with a Wild M5 stereoscopic microscope at 12X, 25X and 50X with 10X ocular. Photographs of sclerotized structures were taken with a Cambridge S-150 "Stereoscan" Scanning Electron Microscope. Photographs of the epipharynx and some structures of the female genitalia were taken with a Reichert-Jung Polyvar compound microscope, and those of other female genital structures were taken with a Zeiss Tessovar macrophotographic unit, both using TMAX 100 black

and white print film.

Methods of phylogenetic reconstruction are discussed in 'Evolutionary Considerations'.

STRUCTURAL FEATURES OF ELATERINI

In this section, character states of the Elaterini I studied are discussed. Character states also are recorded for the taxa of the outgroup of the Elaterini I studied in detail (Sericus, Chiagosnius and Dolerosomus). Not all the character states discussed below were subsequently used in the phylogenetic analysis, since not all character states could be unambiguously defined or confidently polarized. For those character states not used, the distribution of the states in taxa of Elaterini is recorded, since this information cannot be derived from the phylogenetic analysis.

Generic Groups of Convenience

In the course of this study, I have found it useful to recognize four 'groups of convenience' in the Elaterini, each of which includes the type genus of one of the four traditional tribes. The Elater group includes Aphanobius, Neotrichophorus, Pittonotus, Diplostethus, Atractopterus, Leptoschema, Orthostethus, Elater, Parallelostethus, Probothrium, Agelasinus and Ypsilostethus. The Pomachilius group includes Mesembria, Dalopius, Agriotella, Cosmesus, Deromecus, Medonia, Pseudoderomecus, Betarmon, Paracosmesus and Pomachilius. The Agriotes group includes Agriotes (sensu lato). The Adrastus group includes Adrastus, Synaptus, Parasilesis, Ctenoplus, Peripontius, Glyphonyx and Silesis. These group names are intentionally not italicized to distinguish them from names of genera, are used for ease of discussion only to avoid lengthy lists of generic names, and are not intended to designate monophyletic groups.

General Characteristics of Elaterini

In habitus, the Elaterini are typical of most other genera of Elaterinae in being roughly bullet-shaped. The body is subcylindrical in cross section and is more or less markedly tapered towards the apex of the elytra. The body is markedly flattened in only a few species (e.g., Agriotes opaculus LeConte). In most genera, the body is widest around the level of the scutellum. Length of the body ranges from 2-3mm in Panspoeus and some species of Glyphonyx, to 35mm in some species of Orthostethus.

The colours of the Elaterini are various, with a ground colour of various shades of brown predominating. The body is either uniformly ground colour or variously bicoloured. Various shades of red and yellow (rarely green, e.g., Agelasinus viridis Candèze) are present in the bicoloured species. In bicoloured species, the elytra are bicoloured in most species (e.g., Probothrium pubescens Candèze, some species of Dalopius, Mesembria, Smilicerus,

Pomachilius, and others), or the pronotum is bicoloured (e.g., Agriotes fucosus LeConte) or unicolourous but of different colour than the rest of the body (e.g., Ctenoplus collaris Candèze). Colour pattern is species specific in most species.

The body is covered uniformly in a more or less distinct vestiture and variations from this are rare (e.g., body nearly glabrous in Elater abruptus Say; pronotal punctures and setae abruptly more dense posteriorly than anteriorly in Agriotes stabilis LeConte).

Head Capsule and Appendages

Gena. The structural details of the gena have allowed me to divide the Elaterinae into several groups, only one of which, the Elaterini, is hypothesized to be monophyletic.

In species of the tribes Ampedini (Fig. 1A), Megapenthini, Dicrepidiini, Physorhinini and Melanotini I have examined, the ventral margin of the gena is more or less parallel with the ventral margin of the eye; in addition, the anterior margin of the gena below the mandible is clearly visible in lateral aspect, bordered marginally by the carina forming the ventral margin of the gena, and in some species bordered by a submarginal carina. In the Sericosomini (Fig. 1B) and Elaterini (Fig. 1C), the ventral margin of the gena clearly diverges from the ventral margin of the eye. The anterior margin of the gena remains visible in lateral aspect in the Sericosomini (Fig. 1B), but in the Elaterini (Fig. 1C), the ventral margin of the gena forms a sharp border which extends dorsally to the mandible, and the anterior margin of the gena is not clearly visible.

Supraantennal Crests/Frontal Carina. In Elateridae, the antennal socket is bordered dorsally in most taxa by a supraantennal crest which extends from the eye towards the middle of the frons. In some taxa, the supraantennal crests extend completely across the frons (Figs. 1D, E) forming either a rounded projecting rim or a variously projecting carina called the frontal carina. In other taxa, the supraantennal crests curve ventrally toward the anterior margin of the frons (Figs. 1F, G), joining or not joining the anterior margin of the frons. The frontal carina is thus described as complete if the supraantennal crests join each other dorsad the anterior margin of the frons (Fig. 1D), or incomplete if the supraantennal crests do not join each other (Fig. 1G). The configuration of the frontal carina/supraantennal crests shows a great deal of variation within the Elateridae and is considered diagnostic at several taxonomic levels (subfamilies,

tribes, genera; Candèze, 1891, Fleutiaux, 1947). Both complete and incomplete frontal carinae occur in other families of Elateroidea. A complete frontal carina probably has been gained and/or lost repeatedly during the evolution of the Elateridae.

Within the Elaterini, both character states occur. The Pomachiliini are traditionally described as having a complete frontal carina (Candèze, 1860), while Elaterini, Agriotini and Adrastini are traditionally described as having the frontal carina incomplete (Candèze, 1891; Schwarz, 1907). Agriotella Brown, considered to be related to Agriotes by Becker (1956), is placed in the Pomachiliini by European authors (as Idolus Desbrochers) due to the complete frontal carina. Arnett (1962), on the other hand, places Agriotella in the Ampedini (Elaterinae), which also have a complete frontal carina. This disagreement on systematic placement suggests that this character is not an unambiguous indicator of relationship. In Glyphonyx, traditionally an adrastine, the frontal carina is various (Smith & Balsbaugh, 1984), apparently forming a continuous series between complete (Fig. 1E) and incomplete.

The form of the frontal carina is similar in Betarmon, Deromecus, Leptoschema, Medonia, Panspoeus, Pomachilius, Pseudoderomecus and Smilicerus, but the form of the frontal carina in these genera differs from that of Agriotella, Cosmesus, Paracosmesus and Ypsilostethus. In the former eight genera (Fig. 1D), the frontal carina is distinctly separated from the anterior margin of the frons, and the carina is subhorizontal across the frons in anterior aspect; in addition, the frons is flattened immediately posterad the carina, making the frontal carina appear somewhat projecting. In Agriotella, Cosmesus and Paracosmesus (Fig. 1F) the frontal carina is curved ventrally in the middle of the frons, and the frons is not flattened posterad the carina. Thus the frontal carina in the latter three genera is closer to the labrum than in the eight genera discussed above, and the carina is not projecting. In Ypsilostethus, the frontal carina is horizontal and narrowly elevated above the labrum, and the frons is relatively flat from the frontal carina to the vertex.

Periocular space. In the Elaterini, the eye is separated from the antennal socket by section of cuticle of various width (Fig. 1H-J); I refer to this section of cuticle as the periocular space. The cuticle in the periocular space is variously grooved. The depth and shape of the groove exhibits considerable variation in the tribe and further study may reveal useful patterns in this variation. In Glyphonyx (Fig. 1E), Ctenoplus (Fig. 1J), Parasilesis,

Peripontius, Silesis and Synaptus (Fig. 1I), a pair of distinct pits is present in the periocular space ventrad the supraantennal crest; I designate these pits the periocular pits. These pits are relatively deep, steep-walled and subcircular in Glyphonyx, Parasilesis, Peripontius, Silesis and Synaptus (Figs. 1E, I). In Ctenoplus, the pits are shallower and more irregularily shaped (Fig. 1J). The position of the dorsal periocular pit is not the same in New and Old World species of Glyphonyx. In the Old World species of Glyphonyx I have examined, as well as Parasilesis, Peripontius, Silesis and Synaptus (Fig. 1I), the dorsal periocular pit is contiguous with the supraantennal crest; the periocular pit in Ctenoplus is also contiguous with the supraantennal crest. In the New World species of Glyphonyx I have examined, the dorsal pit is distinctly ventrad the supraantennal crest (Fig. 1E).

Antennae. The antennae of most Elaterini are relatively unmodified. Short, erect setae on the antennae of the males (the "secondary male hairs" of authors) are present in many species, but are not necessarily present in the males of all species of a genus. The posterodistal angle of antennomeres 3 or 4 to 10 is variously produced in many species, but in Smilicerus, both the anterodistal and posterodistal angles of antennomeres 4-10 are produced. Antennomeres, and thus the antennae, are various in length. The relative lengths of antennomeres 2 and 3 have been used by some authors to diagnose genera, but in my experience, these two antennomeres exhibit too much variation among species within genera to be useful.

Eyes. Eyes are well developed in all species I have examined, though they are various in size.

Labrum/Epipharynx. In the Elateridae I have examined, the epipharynx bears a pair of distinctly pigmented, flat sclerites arising at the posterolateral margin of the labrum. I refer to these sclerites as the epipharyngeal bar sclerites. In most taxa, only one pair of sclerites is present, but in Agriotes sputator (Linnaeus) an unpaired longitudinal sclerite is present between the posterior ends of the bar sclerites. The epipharyngeal bar sclerites are various in shape, but some patterns are apparent and further study may reveal more patterns.

In the Elaterini, the epipharyngeal bar sclerites are either short antero-posteriorly (Figs. 2A-E) or relatively long antero-posteriorly (Figs. 2F, G). In the former state, the anterior-posterior length of the bar sclerite is less than the median width of the labrum. In the latter state, the anterior-posterior length of the bar sclerite is

subequal to the median width of the labrum.

The relatively short bar sclerites are various in horizontal length. In some genera (Figs. 2A-C), the bar sclerites are relatively short and distinctly separated along the midline of the epipharynx. In other genera (Figs. 2D, E), the bar sclerites are markedly arched basally then extended transversely so that the apices of the sclerites are closer to the midline of the epipharynx. Some patterns are apparent in the structure of the bar sclerites, but differences in detail indicate more study is required. The bar sclerites of Diplostethus are almost identical to those of Probothrium and some New World species of Neotrichophorus (Fig. 2E), and are similar in shape to the bar sclerites of Pittonotus. The bar sclerites of Elater (Fig. 2A) are similar in shape to those of Aphanobius, Leptoschema, Orthostethus, Atractopterus, and, to a lesser degree, Parallelostethus (Fig. 2C). The epipharyngeal bar sclerites of Neotrichophorus depressus (Champion) from Central America, like several other character states, are quite unlike those of other New World species of Neotrichophorus.

The relatively long epipharyngeal bar sclerites are variously divergent posteriorly. In some genera (Fig. 2F), the bar sclerites diverge anteriorly for about three-quarters of their length. In other genera (Fig. 2G), the bar sclerites are subparallel posteriorly for about one-half their length.

Mandibles. The mandibles of Elaterini have proven to be a useful source of previously undescribed character states. In general, the mandibles are relatively robust (Figs. 3E, F) with only two distinct cusps on the occlusal surface. These cusps are various in size, and in some species, are not the same size on the left and right mandibles. The occlusal margin in dorsal aspect is distinctly indented in genera of the Pomachilius, Agriotes and Adrastus groups (Fig. 3F), and is more or less straight in most genera of the Elater group (Fig. 3E). However, these two configurations intergrade. In lateral aspect, the mandibles are distinctly widened anterad the condyles, a widening I designate the basal expansion (Fig. 3B, G). In dorsal aspect, the basal expansion overhangs the dorsal surface, forming a groove which is (Fig. 3F) or is not continuous with the apicolateral groove (Fig. 3E). The basal expansion is always punctate and setate laterally. In taxa of Elaterini I have examined, the apex of the left mandible overrides that of the right mandible when the mandibles are closed.

In the Elateridae, the ventral condyle of the mandible

is situated in one of two positions relative to the dorsal mandibular condyle. In almost all elaterids I have examined, including the Sericosomini, the dorsal and ventral condyles are roughly aligned dorso-ventrally in lateral (Fig. 3A) and ventral aspects. In the Elaterini, the ventral mandibular condyle is situated more anteriorly than the dorsal condyle in lateral (Fig. 3B) and ventral aspects.

In most Elateroidea, including the Sericosomini, the apicolateral surfaces of the left and right mandibles are more or less symmetrical, although one or both mandibles may bear a shallow groove for the reception of the other mandible. In a few genera of the Elaterini, the right mandible is not grooved (Fig. 3E), but in most genera the right mandible has a distinct apicolateral groove (Figs. 3F, G) for the reception of the left mandible and the right and left mandibles are distinctly asymmetrical (Figs. 3G, H). This groove has few punctures and extends to or posterad the basal expansion of the mandibles in lateral aspect (Fig. 3G).

The shape of the posterior end of the apicolateral groove at the basal expansion is various. With the limited number of species examined, patterns were not apparent. However, examination of more species may reveal useful patterns, especially in large genera such as Agriotes (sensu lato).

Depending on the species, the mandibles touch or do not touch each other near the base along a flat surface called the basal face by Acorn and Ball (1991). In taxa whose mandibles contact each other, the basal face appears as a flat, glabrous, smooth and very shiny surface on the occlusal surface of the mandible (under light microscope). The size and shape of the basal face is various (Figs. 3C, D, I, J), and few patterns are evident. The basal face probably has evolved repeatedly in the Elateridae. In the Elaterini, the basal face is very small or absent from the type species of Elater, and the type species and some New World species of Neotrichophorus (Fig. 3C). In other Elaterini, the basal face appears to form a continuous grade between relatively narrow and relatively wide. Although the basal face in some New World species of Neotrichophorus is very small or absent, that of Neotrichophorus depressus from Central America is relatively large and wide.

Within the Elaterini, a unique appearance of the basal face is seen in Adrastus, Ctenoplus, Glyphonyx, Parasilesis, Peripontius, and Silesis, and a variation of this is seen in Synaptus. In the first six genera, the

anteroventral margin of the basal face bears a pronounced tooth (Fig. 3I). In Synaptus, the anteroventral margin bears a pronounced flange (Fig. 3J).

In those taxa with a pronounced flange or tooth on the basal face, Synaptus and Peripontius have the flange or tooth in the same plane as the rest of the basal face. Adrastus, Ctenoplus, Glyphonyx (Fig. 3K), Parasilesis and Silesis have the tooth directed occlusally (at approximately right angles to the rest of the basal face).

In most Elateridae I have examined, the dorsal surface of the mandible adjacent to the basal face bears a relatively large, semicircular, fringed area (Figs. 3E, F) that appears membranous or semimembranous under light microscope. In Pseudoderomecus and some species of Agriotes (Ectinus), this membranous area is reduced to a smaller, more central membranous patch on the dorsal surface, and in Adrastus, Agriotella, Agriotes (sensu stricto), Betarmon, Cosmesus, Dalopius, Deromecus, Paracosmesus, Peripontius, Pomachilius, Silesis and Synaptus, the membranous area has become completely sclerotized. The remaining taxa of Elaterini have the large membranous area described above.

In the Elaterini, the terebral tooth (sensu Acorn & Ball, 1991) of the right mandible in occlusal aspect is either relatively small (Fig. 3C), or is relatively large (Figs. 3D, I, J).

In most Elaterini, the basal expansion of the right mandible is more or less flat dorsoventrally. In Diplostethus, New World species of Neotrichophorus (Fig. 4A) and Orthostethus, the right mandible has a distinct crest, subparallel with the ventral margin of the mandible, between the dorsolateral groove and the ventral margin of the mandible.

The anterior margin of the basal expansion of the left mandible is either directed anteroventrally or ventrally, thus appearing relatively oblique (Fig. 4B) or relatively perpendicular (Fig. 4C), respectively.

The lateral surface of the left mandible shows several configurations and further study may reveal useful patterns. The anterior margin of the basal expansion of the left mandible in Smilicerus and many species of Pomachilius is almost vertical and bears a low rounded crest that extends to the ventral margin of the mandible. This configuration is present in Smilicerus sallei Candèze, S. zonatus Candèze, Pomachilius spinifer Champion, P. suturalis Candèze, P. linearis Candèze, P. hiosurus

Candèze, P. cuspidatus Candèze and 8-10 other unidentified species of Pomachilius. I have also seen five or six unidentified species of Pomachilius in which the anterior margin is curved posteriorly, extending or not to the ventral margin of the mandible. This latter configuration is present (more or less) in Agriotella, Cosmesus, Dalopius, Agriotes fucosus LeConte (a member of subgenus Ectinus), Deromecus, Betarmon and Paracosmesus.

The configuration in which the anterior margin of the basal expansion is curved posteriorly as a more or less distinct crest described in the paragraph above grades into a configuration in which the basal expansion is grooved ventrally, and the groove is more or less limited dorsally by a crest that is continuous with the anterior margin of the basal expansion. This latter configuration is present in Silesis, Synaptus, Agriotes isabellinus Melsheimer (a member of the Sparsus group) and Cosmesus. Unassignable intergrades between the two configurations described in this paragraph are present in some species of Agriotella, Dalopius, Peripontius and Parasilesis.

The lateral margin of the left mandible is more or less evenly convex from the posterior to anterior end of the basal expansion in most Elaterini, and shows little modification. In a few genera, the lateral margin of the left mandible bears a relatively large, well-defined pit at the anterior margin of the basal expansion. The development of the pit is variable in Pittonotus theseus (Germar), but is visible in all specimens I have examined. Unfortunately, the pit is best high-lighted by shadows cast by the margin of the pit under light microscopy. I have not been able to reproduce this effect on scanning electron micrographs.

Maxilla. The sclerites of the maxilla are relatively unmodified in the Elaterini (Figs. 4D, E). The cardo, basistipes and mediostipes are distinctly sclerotized and variously setate. The galea and lacinia are semimembranous and bear a thick covering of fine setae. The maxillary palpi are four-articled. The terminal palpomere is various in shape, but this may be species-specific.

In the Elaterini, the basistipes either bears more than one seta that is at least as long as the basistipes itself (Fig. 4D), or the basistipes bears only one very long seta that is much longer than the basistipes (Fig. 4E). In the latter state, this very long seta is centrally placed in most taxa, but shorter setae are also present, especially laterally.

Within the Elaterinae, the lacinia is various in size

and shape (Guryeva, 1979b, figs. 40-44). I have not found a difference in shape of the lacinia in the Elaterini, but the size is various. In most taxa, the lacinia is relatively short, with the apex of the lacinia subequal with the level of the apex of the ventral sclerite of the galea. In Agriotes (Ectinus), Cosmesus, Elater, Parallelostethus, Pittonotus and Probothrium, the lacinia is relatively long, with the apex of the lacinia anterad the level of the apex of the ventral sclerite of the galea. The character state in Deromecus, Medonia, New World species of Neotrichophorus and Orthostethus appears to be variously intermediate between long and short.

The ventral surface of the galea is variously sclerotized in the Elaterini. The ventral surface of the galea bears a single sclerite that extends horizontally across the ventral surface of the galea in most taxa of Elaterini, as well as Sericus. However, the size and shape of the sclerite is not the same in all taxa. In several taxa (e. g., Agelasinus), the sclerite is much narrower along the midline, and in most, the lateral half is less heavily sclerotized. The character is not consistent within Agriotes. Agriotes (Ectinus) and the Sparsus group have a single horizontal sclerite, as above. Two configurations are present in the Sputator group. In A. sputator (Linnaeus), two sclerites separated along the midline are present, while in A. mancus (Say), a single horizontal sclerite greatly constricted at the midline is present. Two ventral sclerites separated along the midline of the galea are also present in Adrastus, Parasilesis and Peripontius. In Diplostethus, Glyphonyx, New World species of Neotrichophorus, Pomachilius, Probothrium and Silesis, as well as Chiagosnius and Dolerosomus, the ventral surface of the galea bears only a single sclerite on the mesal side of the midline; this configuration is present in other taxa of the subfamily Elaterinae (e.g, some species of Megapenthes Kiesenwetter, and Melanotus Eschscholtz).

Labium. Like the maxilla, the labium is relatively unmodified. No character states have been identified.

PROTHORAX

The prothorax in the Elaterini is variously subrectangular in dorsal aspect, and forms a continuous grade between distinctly wider than long in some species of Agelasinus to distinctly longer than wide in many species of Pomachilius. The lateral margins in dorsal aspect form a continuous grade between distinctly converging anteriorly (e.g., Atractopterus, Parallelostethus) to modestly diverging anteriorly (e.g., Dalopius). The lateral carina of the pronotum is always present, though it is interrupted

in some taxa (e.g., Medonia, some species of Agriotes). The hind angles of the pronotum are variously elongated and, in most genera, bear one (or rarely two) carina. In the species I have examined, the prothorax is punctate throughout, but the density and spacing of the punctures are various. In most species, pronotal punctures are larger and more closely spaced near the lateral margin. In most species the size of the punctures is approximately uniform from the anterior to posterior margin, but the posterior pronotal punctures are distinctly smaller in Agriotes stabilis LeConte and some specimens of Ctenoplus nitidipennis Schwarz.

Anterior subpronotal lobe. The pronotum in Elaterini bears a variously sclerotized and emarginate lobe along the anterior margin at the line of attachment of the intersegmental membrane (Figs. 4F-I). I designate this lobe the anterior subpronotal lobe. The lobe is best seen when the head is disarticulated from the prothorax, the prothorax has had soft tissue removed, and viewed from anterior or anteroventral aspect. The lobe is either indistinctly sclerotized and its emargination relatively shallow and smoothly curved (Figs. 4F-H), or the posterior margin is more distinctly sclerotized than the rest of the lobe and has a relatively deep, subquadrate emargination (Fig. 4I). The former character state is present in Agelasinus, Aphanobius, Atractopterus (Fig. 4F), Diplostethus (Fig. 4H), Elater, Leptoschema, New and Old World species of Neotrichophorus (Fig. 4G), Orthostethus, Parallelostethus, Pittonotus and Probothrium, but the size and degree of sclerotization of the lobe in these taxa is various. The lobe is very small and difficult to find in Atractopterus (Fig. 4F), but is larger, more distinctly sclerotized, and thus easier to see in the other genera (Figs. 4G, H).

Lateral carina. Within the Elaterini, the lateral carina of the pronotum either joins the anterior margin of the pronotum distinctly dorsad the point at which the mesal margin of the hypomeron joins the anterior margin of the pronotum (Figs. 5C, D), or the lateral carina and the mesal margin of the hypomeron join the anterior margin of the pronotum at, or very close to, the same point (Figs. 5A, B). In most species the distinction between these two states is unambiguous, but in a few, the lateral carina may join the anterior margin slightly but noticeably dorsad the mesal margin of the hypomeron.

Hind angles. The posterolateral angles of the pronotum are variously produced in Elateridae and are referred to as the hind angles (Fig. 5C). In the Sericosomini and some Elaterini, the hind angles of the pronotum bear an

apical/subapical tuft of stouter setae directed posterolaterally (Fig. 5G). In Dolerosomus (Sericosomini), the setae are relatively long, while in Sericus (Sericosomini), they are relatively short. Kishii (1987) used the presence of these setae to segregate groups of genera in the Japanese traditional Elaterini. According to Kishii (1987), long setae are present in Neotrichophorus, Elater and Parallelostethus (treated as a subgenus of Elater), and setae are absent from Sericus, Vuilletus, Chiagnosius and Dolerosomus. Caution must be used when assessing this character, since the setae appear to be easily lost, and are various in position (they can be lateral, dorsal or apical on the hind angles). The setae are more apparent on pinned specimens than alcohol-preserved specimens. A series of specimens needs to be examined before the absence of these setae is confirmed. In other genera of Elaterini, the stouter setae near the apex of the hind angles are more dispersed, usually on the mesal side of the hind angles (though apical in some species) and are directed posteriorly towards the humeral angle of the elytra.

Mesal margin of hypomeron. In Sericosomini and most Elaterini, the pronotosternal sutures traditionally and erroneously are described as "double". As argued by Hayek (1990), the descriptor used is quite inaccurate: there is only one suture present between the prosternum and the hypomeron, and the character state being described does not involve the pronotosternal sutures at all. Hayek (1990:45) prefers "inner margin of hypomeron with a well defined narrow, completely or almost completely impunctate border" (Fig. 5F) to describe what are traditionally described as "double pronotosternal sutures". In the character state traditionally described as "single pronotosternal sutures", this differentiated border has been lost posteriorly and the punctation of the hypomeron continues to the margin adjacent to the prosternum (Fig. 5E). The impunctate mesal margin of the hypomeron is absent from Aphanobius, Diplostethus (Fig. 5E), Elater, New and Old World species of Neotrichophorus, Parallelostethus and Pittonotus.

This character is not consistent within Parallelostethus or New World species of Neotrichophorus. The type species of Parallelostethus lacks the impunctate border of the hypomeron, while P. acutus (Candèze) from southeast Asia has the impunctate border. This difference traditionally has been considered diagnostic of genera in the Elateridae. Some New World species of Neotrichophorus have an impunctate border (e.g., N. physorhinus (Candèze)), while other species vary between punctate and impunctate (e.g., N. carolinensis (Schaeffer) and N. depressus (Champion)).

Pronotosternal sutures. In Elateridae, the hypomeron and prosternum contact along the pronotosternal sutures (Fig. 5C). The sutures are rigidly fused posteriorly, but a certain amount of movement is possible anteriorly. Whether or not the pronotosternal sutures are straight or curved ectally was used by Schwarz (1906, 1907) to segregate groups of genera in both the traditional Pomachiliini and Steatoderini (a synonym of Elaterini). In the taxa I have examined, the pronotosternal sutures are clearly curved ectally in Agriotella, Agriotes (Ectinus), Atractopterus, Betarmon, Deromecus, Leptoschema, Medonia, Pomachilius and Pseudoderomecus, as well as Sericus and Dolerosomus. The pronotosternal sutures are close enough to straight in Agriotes (sensu stricto), Aphanobius, Cosmesus, Ctenoplus, Orthostethus, Paracosmesus, Parasilesis, Peripontius, Pittonotus, Probothrium, Silesis, Synaptus and Ypsilostethus. In Adrastus, Agelasinus, Dalopius, Diplostethus, Elater, Glyphonyx, New and Old World species of Neotrichophorus and Parallelostethus, the pronotosternal sutures are variously intermediate between the above two states.

Prosternum. In the Elateridae, Cebrionidae and Eucnemidae examined, the prosternum bears an anterolateral projection at the base of the prosternal lobe. It is best seen when the prothorax is disarticulated from the head and soft tissue is removed.

In ventral aspect, this projection is variously prominent. In sericosomines, the projection is truncated and barely, or not visible, as it is in some Elaterini (Fig. 5E). In other Elaterini, the anterolateral projection of the prosternum is readily visible (prominent) in ventral aspect, and acute or rounded apically (Fig. 5F).

In Sericosomini and most Elaterini, the anterolateral projection of the prosternum is elongated dorsolaterally in anterior aspect (Fig. 4H). In a few Elaterini, the anterolateral projection is flattened (Fig. 4G).

Prosternal mucro. In Elateridae, the prosternum bears a variously elongate projection between the procoxae called the prosternal mucro (Fig. 5C). The shape of the ventral surface of the prosternal mucro has been used by Champion (1895) and Schwarz (1907) to define subgroups or genera within the traditional Elaterini. Specifically, a horizontal ventral margin (Fig. 6A) is diagnostic of Elater, a gradually declivous ventral margin (Fig. 6B) is diagnostic of Neotrichophorus and an abruptly declivous ventral margin (Fig. 6C) is diagnostic of Diplostethus. More recently, Kishii (1987) has used the position of the

subapical tooth (Fig. 6D) to define subgenera within the Japanese species of Elater. I have not found the shape of the ventral surface to be phylogenetically useful, but it is useful for diagnosing some genera. When all the taxa within the Elaterini are compared, there appears to be a continuous grade between a more or less concave ventral surface (gradually declivous, e.g., Fig. 6B) and a more or less convex ventral surface (e.g., Fig. 6D). I have concluded that the disinction between more or less concave and more or less horizontal, and more or less horizontal and more or less convex is more or less arbitrary, especially in species of Adrastus, Ctenoplus, Dalopius and Peripontius, as well as Sericus and Dolerosomus.

In some taxa, the shape of the ventral surface might be used as an autapomorphic character. Diplostethus has a more or less perpendicular "step" between the procoxae and the subapical tooth (Fig. 6C). In Agelasinus, the ventral margin slopes abruptly dorsally immediately posterad the procoxae (Fig. 6E).

In Pittonotus, Orthostethus and Elater (Nipponoelater Kishii), the subapical tooth is situated more or less at the midpoint of the prosternal mucro (as in Fig. 6D), although its exact position is various in both Orthostethus and Elater (Nipponoelater). Further study is required of the species of Orthostethus and Elater before the position of the subapical tooth can be considered diagnostic of these taxa.

The shape of the prosternal mucro was used by Guryeva (1979b) and Ohira (1990) to diagnose genera in the Adrastus group (see key).

Proendosternite. In most Elaterini, and almost all other Elateridae I have examined, the procoxal cavities are open dorsally to the body cavity (Fig. 7A). This character is visible only in posterior aspect and requires disarticulating the prothorax from the mesothorax. In Adrastus, Agriotes (sensu stricto) (Fig. 7B), Glyphonyx, Ctenoplus, Parasilesis, Peripontius and Silesis, the procoxal cavities are closed dorsally by lateral extensions of the proendosternite.

MESOTHORAX

Structures of the mesothorax of some Elaterinae were studied by Guryeva (1974), but apparently provided no character states which allowed her to diagnose tribes within this subfamily. Calder (1986) used some character states of the mesonotum and mesosternum to diagnose genera within the Crepidomeninae. My examination of the mesonotum

to date has been inconclusive, perhaps due to problems of monophyly. Examination of more species may identify useful patterns within the genera of Elaterini.

The scutellum is always distinct, but various in size, shape and angle of inclination. Elytra are always fully developed, variously excavated around the scutellum, variously punctato-striate, with the apices various in shape. The apices of the elytra are variously rounded, truncate, notched or attenuated. In some species, the sutural margins of the elytra are produced into spines at the apex, and in some species with notched apices, the outer and/or sutural margins of the notch are produced into spines. In almost all species examined, the modifications of the apex of the elytron are specific to that species.

Sclerites of the ventral surface of the mesothorax are shown in Fig. 9D.

Mesosternum. The mesosternum in Elateridae bears a distinct deep pit for the reception of the prosternal mucro; this pit is called the mesosternal fossa (Fig. 9D).

In the Sericosomini and some Elaterini, the margins of the mesosternal fossa are relatively unmodified. The margins of the fossa are variously raised, various in thickness, sharp (Fig. 7C) or variously rounded (Fig. 7H). In other genera of Elaterini, the margins of the mesosternal fossa are raised, thin and at least partially crenellated (Fig. 7D).

The shape of the margins of the mesosternal fossa was used by Schwarz (1906, 1907) to distinguish between genera and groups of genera within the traditional tribes Pomachiliini, Adrastini and Elaterini (including Agriotini). In Agelasinus, Aphanobius, and Leptoschema, as well as Sericus and Dolerosomus, the margins of the fossa are slightly raised posteriorly beginning at the anterior margin of the mesocoxae. In Atractopterus and New World species of Neotrichophorus, the margins of the fossa are slightly raised posteriorly, but this begins near the midpoint of the mesosternum. In Probothrium, the posterior margin of the mesosternum between the mesocoxae is almost perpendicular from the meso-metasternal suture to the posterior margin of the mesosternal fossa. Old World species of Neotrichophorus and some New World species of Neotrichophorus are intermediate between the slightly raised condition of Aphanobius and that of Probothrium. The distinction between the slightly raised condition and that of Probothrium appears to represent the ends of a gradient.

In several genera, the margins of the mesosternal fossa are raised and more or less horizontal between the mesocoxae, but the shape of the fossal margin anterad the horizontal portion is various. In Orthostethus (Fig. 7E) and Ypsilostethus, the margin is almost perpendicular just anterad the level of the anterior margin of the mesocoxae. In Parallelostethus, the margins are raised gradually beginning near the anterior margin of the mesosternum (Figs. 7H, 8F). In some species of Diplostethus, Elater and Pittonotus, the margins rise at about a 45 degree angle beginning at the level of the anterior margin of the mesocoxae. However, after examining several other species of Orthostethus, Elater and Diplostethus, I am not convinced this character is consistent within these genera. In the latter three genera, a useful character state may be present, but determining this must await revision of those genera.

The margins of the mesosternal fossa are raised and more or less horizontal between the mesocoxae in Ctenoplus (Fig. 7F), Glyphonyx, Parasilesis, Peripontius and Silesis, but the crenellate fossal margins anterad the horizontal portion are more convex than in Diplostethus, Elater, Orthostethus, Pittonotus and Ypsilostethus.

In Adrastus (Fig. 7G), Agriotes, Agriotella, Betarmon, Cosmesus, Deromecus, Paracosmesus, Pomachilius, some species of Pseudoderomecus, and Synaptus, the crenellated fossal margins are distinctly convex, reaching their apex just anterad the mesocoxae. The condition in Ctenoplus, Glyphonyx, Parasilesis, Peripontius and Silesis is described above. The character state in Dalopius, Medonia, and the type species of Pseudoderomecus is intermediate between the above two groups.

In Agelasinus, Agriotes, Aphanobius, Atractopterus, Elater, Glyphonyx (Fig. 8A), Leptoschema, Paracosmesus, Peripontius, Silesis, Synaptus and Ypsilostethus, the margins of the mesosternal fossa are more or less convex in ventral aspect. In Agriotella, Betarmon, Ctenoplus, Diplostethus, New and Old World species of Neotrichophorus (Figs. 8B, C), Parallelostethus (Fig. 8F), Parasilesis, Pittonotus, Pomachilius and Probothrium, the margins of the mesosternal fossa are more or less subparallel in ventral aspect. In Adrastus, Cosmesus, Dalopius (Fig. 8D), Deromecus, some species of Glyphonyx, Medonia and Orthostethus, the margins of the mesosternal fossa are intermediate between more or less convex and more or less subparallel in ventral aspect, and can not be placed in either state without being arbitrary.

Taxa differ notably in the shapes of the anterior

margin of the mesosternum and the posterior margin of the mesosternal fossa, but the configurations are largely taxon-specific and I have not been able to identify any patterns. These areas may provide valuable diagnostic characters for genus-group taxa.

In Atractopterus, Diplostethus, Elater and New World species of Neotrichophorus (Fig. 8C), as well as Sericus, the mesosternal fossa bears an inverted Y-shaped groove anteriorly. In Atractopterus, the posterior branches are much shorter than in Sericus, Diplostethus, Elater, New World species of Neotrichophorus and Sericus. In Chiagosnius, Dolerosomus and all other taxa of Elaterini, this groove is absent.

In Sericosomini and most Elaterini, the lateral lobes of the mesosternum (sensu Guryeva, 1974) are slightly concave without deeper secondary depressions. In Aphanobius, Ctenoplus, Mesembria, Old World species of Neotrichophorus, Pseudoderomecus and Ypsilostethus, the lateral lobes of the mesosternum bear a secondary depression. In Aphanobius, the depression occupies the anterior half of the lateral lobes (Fig. 8E). In the latter five taxa, the depression is restricted to the mesolateral margin of the lateral lobes; it is subcircular and bounded posteriorly by a sharp ridge in Old World species of Neotrichophorus (Fig. 8B), and subreniform in Ctenoplus (Fig. 7F), Mesembria, Pseudoderomecus and Ypsilostethus.

In Elateridae, the anterior margin of the mesosternum is excavated laterad the mesosternal fossa; this area is referred to as the anterior articulating surface by Guryeva (1974) (Fig. 9D). The anterior articulating surface either occupies part of the anteroventral surface of the mesosternum (Figs. 8A, D), or is restricted to the anterior surface of the mesosternum (Fig. 8C).

Mesepimeron. In all but one of the taxa of Elaterini, the mesepimeron bears a distinct anterolateral projection (Fig. 8G) that contacts the humeral angle of the elytra. In Atractopterus, the anterolateral mesepimeral projection is virtually absent (Fig. 8H).

Also in Atractopterus, the setae of the mesepimeron arise on tubercles (Fig. 8H). In all other taxa of Elaterini and Sericosomini, the mesepimeral setae arise in pits (Fig. 8G).

METATHORAX

Metathoracic wings are fully developed in all species

I have examined, but one species, Microglyphonyx coarctatus Champion, is apterous (Champion, 1896). Wing venation in Elateridae has been studied by Dolin (1975), who proposed a classification of the family based in part on this character. However, wing venation is known to vary within species (Hawkins, 1936), and I prefer to defer comments on venation until patterns within genera can be established.

Metasternum. The metasternum is fully developed in all species I have examined but is reduced in Microglyphonyx coarctatus (Champion, 1896).

Median groove. In almost all taxa of Elaterini and Sericosomini, the metasternum bears a median sulcus that extends from the metacoxal plates almost to the mesocoxae (Fig. 9A), and is visible as a distinct groove on the midline. In Parasilesis, the metasternal sulcus is present only posteriorly near the metacoxal plates (Fig. 9B). In Ctenoplus, Glyphonyx (Fig. 9C), Peripontius and Silesis, the metasternal sulcus is absent.

Lateral groove. The anterior margin of the metasternum in Elaterini is bounded anteriorly by a low flat marginal ridge between the mesocoxal cavities and the metepipleuron (Fig. 9D). This ridge continues posteriorly along the lateral margin of the metasternum for various distances, and in some taxa, almost meets the posterior margin of the metasternum. In some taxa, the marginal ridge bears an oblique, acute extension of various length posterad the mesocoxal cavities (Figs. 7F, 9C). The marginal ridge is bordered on the metasternum by a submarginal groove (Fig. 9E) which also continues posteriorly for various distances parallel with or slightly converging on the marginal ridge. The length of the submarginal groove laterally may be diagnostic for some taxa, but further study is required. A relatively long lateral groove is present in all genera of the Adrastus group, most taxa of the Agriotes group (except the Sparsus group of Agriotes), Deromecus, Mesembria and Ypsilostethus. It is also found in a few species of Pomachilius (but absent from most), one species of Agelasinus (but absent from others including the type species) and present but various in length in some Old World species of Parallelostethus (but absent from the New World type species and other Old World species).

LEGS

Legs of species of Elaterini are relatively unmodified and seem adapted for walking or running. Fossorial or other specific adaptations were not observed in the specimens I examined. In general, the mesothoracic legs are somewhat longer and thinner than the prothoracic legs,

and the metathoracic legs are somewhat longer than the mesothoracic legs.

Mesotrochantin. Three states of the mesotrochantin were observed in the Elaterini. In Sericosomini and some Elaterini, the mesotrochantin is approximately twice as long as its median width in ventral aspect (Fig. 8C); as a result, the posterolateral margin of the mesosternum is relatively long and truncate, and the mesepisternum forms part of the margin of the mesocoxal cavity between the mesosternum and mesepimeron. In the remaining taxa of Elaterini, one of two configurations is present. In most genera, the mesotrochantin is only about as long as its median width in ventral aspect (Fig. 8D); thus the posterolateral margin of the mesosternum is relatively short but still truncate, and the mesepisternum forms or does not form part of the mesocoxal cavity between the mesosternum and the mesepimeron. In the other genera, the mesotrochantin is concealed or nearly concealed by an extension of the mesepimeron (Fig. 8A); thus the posterolateral margin of the mesosternum is very short and bluntly rounded, and the mesepisternum does not form part of the margin of the mesocoxal cavity.

Metacoxal plate. In Elaterini, the posterior margin of the metacoxal plate bears a distinct tooth at the level of the trochanter-femur joint (Fig. 9F). This tooth is various in size and pointedness, and grades into the indistinctly rounded state found in most taxa (Fig. 9G).

Tarsomeres. In the Elateroidea, two forms of tarsomeres are recognized: those described as "simple" and those described as "lobed". Simple tarsomeres (Fig. 10A) have the ventral surface variously setose or "felty", and the distal end of the tarsomeres are oblique. Lobed tarsomeres also have the ventral surface variously setose, but the ventrodistal end of at least one tarsomere is produced into a more or less distinct, setose, dorsoventrally flattened lobe (Figs. 10B-D). At present, it is not possible to determine the ancestral condition for the Elateridae. Both lobed and simple tarsomeres are found in the Eucnemidae and Throscidae. Cebrionidae appear to have simple tarsomeres. Within the Elateridae, the number and distribution of lobed tarsomeres have been used as diagnostic characters at several taxonomic levels, and traditionally are considered diagnostic of genera, at least. Few tribes in the family do not contain at least one genus with at least one tarsomere bearing a lobe. As diagnostic characters and indicators of relationship, the presence or absence of lobes on the tarsomeres appears to be questionable (Becker, 1972). Lobes on tarsomeres probably have been gained and/or lost repeatedly during the evolution of the

Elateridae.

Within the Elaterini, lobed tarsomeres are found in some genera of the Pomachilius and Adrastus groups and Pseudagriotes. In genera with lobed tarsomeres, most have either tarsomere 3 or 4 lobed. However, tarsomeres 3 and 4 are lobed in Old World species of Glyphonyx (Fig. 10D) (Fleutiaux, 1940c), but only tarsomere 4 is lobed in New World species of Glyphonyx (Fig. 10C) (Smith and Balsbaugh, 1984). Traditionally, this difference in number of lobed tarsomeres would warrant generic distinction.

Tarsal claws. In most Elateroidea, the tarsal claws are unmodified and called 'simple' (Fig. 10E). Simple tarsal claws are present in Sericosomini and most Elaterini. Two modifications are observed within the Elaterini. In Ypsilostethus, each tarsal claw bears a large, subtriangular basal projection (Fig. 10F), a configuration described as "flanged" by Stibick (1971) and toothed by other authors. In the Adrastus group (Fig. 10G), the tarsal claws bear multiple teeth, like the teeth of a comb, and traditionally are called "pectinate". Stibick (1979) described the tarsal claws of the traditional Adrastini as "serrate" and applies the term "pectinate" to the Melanotinae and unspecified taxa of Denticollinae and Cardiophorinae, but does not explain his concept of "serrate" and "pectinate". I am unable to make a consistent distinction between the two states on specimens of the taxa referred to above, and use the term "pectinate" for tarsal claws that bear multiple teeth.

ABDOMEN

The abdomen in most taxa of Elaterini lacks any obvious modification. In some species, the apex of sternum VII is produced into a distinct spine. In some taxa, (e.g., Ctenoplus), the abdominal terga are distinctly more sclerotized.

MALE GENITALIA

External genitalia of Elaterini are typical of the "generalized, bilaterally symmetrical, trilobed form" of Zacharuk (1958a). In some taxa, the parameres bear a lateral, subapical, variously acute tooth, while in others, the parameres are more or less evenly rounded apically. As usual, intergrades between these two states exist (e.g., some species of Pomachilius). This character may reveal useful patterns for phylogenetic analysis, but male genitalia are species specific for most species. I am reluctant to make any generalizations based on the limited number of species examined in this study. Internal organs

of reproduction were not studied since most of these are destroyed by potassium hydroxide. Brown & Keaster (1978) found species specific differences in the internal reproductive glands of some species of Melanotus, and useful patterns may yet be found in the Elaterini.

FEMALE GENITALIA

Abdominal Segment VIII. In some taxa of Elaterini (e.g., Diplostethus, Probothrium), sternum VIII is distinctly narrower than tergum VIII, while in most taxa, sternum VIII and tergum VIII are subequal in width. These two character states are not discrete, and various intermediate states exist (e.g., Parasilesis, Ctenoplus).

In Agriotella, Agriotes (sensu stricto), Atractopterus, Dalopius, Elater, Orthostethus, Parallelostethus, Pittonotus and Pomachilius, as well as Sericus, sternum VIII bears a large lateral glabrous area of various size and shape posterad the apodemes. In most other Elaterini, as well as Chiagosnius and Dolerosomus, sternum VIII is more or less uniformly setate. In Deromecus, Mesembria, Paracosmesus and Pseudoderomecus, a smaller glabrous area of various size and shape is present. This patch is bilaterally symmetrical or not in Deromecus. The presence of this glabrous area is not consistent in Dalopius. The type species has a large glabrous areas, but D. cognatus Brown has sternum VIII uniformly setate.

In most taxa of Elaterini, the apodemes of segment VIII gradually diverge posteriorly beginning anterad the level of spiracle VIII (Fig. 10K). In a few taxa (e.g., Elater and Orthostethus), the apodemes diverge rather abruptly posteriorly beginning near the level of spiracle VIII. The point at which divergence begins and the degree of divergence are various in other taxa.

In most taxa of Elaterini, the apodemes of segment VIII are curved laterally to form part of the posterior margin of sternum VIII (Fig. 10K). In Probothrium, the apodemes do not form part of the posterior margin of sternum VIII. The apodemes of Diplostethus, New and Old World species of Neotrichophorus and Agriotes mancus (Say) (a member of the Sputator group) appear to be intermediate between the above two states.

Spiracular sclerite of segment VIII. In Sericosomini and most Elaterini, the spiracle of segment VIII lacks any discernable posterior border, or has a very short anteromesally directed bar sclerite (e.g., Agelasinus). In some genera of Elaterini, the spiracle of segment VIII has a relatively large and distinct posterior border (Fig.

10K). The appearance of this border is various, and possibly taxon-specific.

Ovipositor. Terms for the sclerites of the female genital appendages proposed by Tanner (1927) were applied to the sclerites of the ovipositor of a species of Elateridae by Zacharuk (1958a). Most of these are adopted here for the Elaterini and are shown in Figs. 10H-J, with the following exceptions; I have followed Lawrence & Britton (1991) in using 'baculus' instead of 'second valvifer'.

In most genera of Elaterini, the stylus of the gonocoxites is present and situated virtually at the apex of the apical part of the gonocoxites (Fig. 10H), as it is in Chiagosnius and Dolerosomus (Sericosomini). In a few genera of Elaterini, the stylus is separated from the apex of the apical part of the gonocoxites by at least half the length of the stylus (Fig. 10I).

In Atractopterus, the apical part of the gonocoxites bears an abrupt shoulder immediately anterad the lateral tuft of setae. The character states in Parallelostethus, Pittonotus and Probothrium appear to be intergrades between shouldered and unshouldered states.

In many taxa, the apical part of the gonocoxites is distinctly narrowed near the midpoint, while in others, the lateral margin of the apical part of the gonocoxites is more or less straight. However, these two states intergrade.

In Atractopterus, Diplostethus, Elater, New World species of Neotrichophorus, Orthostethus, Parallelostethus (Fig. 10I), Pittonotus and Probothrium, as well as Sericus, the baculi are expanded laterally forming a sclerotized, but more lightly pigmented, lateral wall of the ovipositor. In the remaining Elaterini and Sericosomini, the baculi are thin, ventral and rod-like, leaving the lateral wall of the ovipositor membranous.

Tergum X is situated between the posterior ends of the baculi, immediately anterad the gonocoxites (Fig. 10I). In most genera of Elaterini and Sericosomini, tergum X is relatively small (though various in size and shape) and very lightly pigmented. In Atractopterus, Diplostethus, Elater, New World species of Neotrichophorus, Orthostethus, Parallelostethus, Pittonotus and Probothrium, as well as Sericus, tergum X is relatively large (though again, various in size and shape), occupies the dorsal surface between the posterior half of the baculi (Fig. 10I), and is more heavily pigmented, except in Diplostethus and New World species of Neotrichophorus. In the taxa with a more

heavily pigmented tergum X, the tergum is membranous for most of its length along the midline, and appears U-shaped; this is not as obvious in Diplostethus, New World species of Neotrichophorus and Sericus, but appears to be the same.

In most taxa of Elaterini, as well as Chiagosnius and Dolerosomus, a suture is visible between the basal and apical parts of the gonocoxites (Fig. 10J). The suture is present on the ventral surface only, is diagonal, and in most taxa is situated at about the level of the vulva. However, the position of the suture is various. In some taxa, it is posterad the vulva, while in others, it is anterad the vulva. The suture is more easily seen in taxa with heavily pigmented gonocoxites, and can be quite difficult to find in taxa with lightly pigmented gonocoxites (Fig. 10H). In the latter group, the suture appears as a narrow, ventral impression or small, lateral notch near the level of the vulva. In Atractopterus, Parallelostethus (Fig. 10I) and Sericus, no suture is visible.

In Elater, Orthostethus, Parallelostethus (Fig. 10I), Pittonotus and Probothrium, as well as Sericus, the apical part of the gonocoxites lacks both an apical tuft of setae and scattered long setae anterad the stylus. In the other genera of Elaterini and Sericosomini, the apical part of the gonocoxites bears an apical tuft of setae, and has scattered long setae anterad the stylus (Fig. 10H).

In Atractopterus, Elater, Orthostethus, Parallelostethus, Pittonotus and Probothrium, as well as Sericus, the gonocoxites are completely or almost completely sclerotized and darkly pigmented (Figs. 10 I, J). In the other genera of Elaterini and Sericosomini, heavy sclerotization is restricted to narrow longitudinal bands dorsally and laterally, and a narrow horizontal band anteroventrally on each gonocoxite.

Vagina. In some species of Agriotella and Cosmesus, the vagina bears a pair of elongate sclerotized plates. These plates are more heavily sclerotized and lie beside each other perpendicular to the long axis of the vagina in Cosmesus, whereas in Agriotella, the plates are less heavily sclerotized, appear striated and lie beside each other parallel to the long axis of the vagina. The plates are longer in Agriotella than in Cosmesus, but otherwise are similar in shape and position. However, the presence of the plates is not consistent in Cosmesus; they are absent from the type species.

Bursa copulatrix. Becker (1958) drew attention to the usefulness of the female internal organs of reproduction as

indicators of relationship in at least some genera of Elateridae. Within the Elaterini, I have found the structure and armature of the bursa copulatrix useful in this regard.

The bursa copulatrix in Sericosomini is roughly straight with the spermathecal duct arising at the anterior end. This configuration is also seen in Aphanobius, Old World species of Neotrichophorus and Pittonotus, although the bursa is more convoluted in Aphanobius. In the specimens I have examined, other configurations are evident, though the literature suggests some of these may not be discrete. In Diplostethus and New World species of Neotrichophorus (Fig. 11B), the bursa is still roughly linear with the spermathecal duct arising anteriorly, but the bursa is distinctively coiled. In Orthostethus and Parallelostethus, the bursa is also roughly linear with the spermathecal duct arising anteriorly, but the accessory gland arises from an enlargement of the bursa near the middle (Fig. 11C). In the remaining genera of Elaterini, the bursa is more U-shaped, with the spermathecal duct arising more posteriorly (Fig. 11E).

The species I studied as an example of Glyphonyx [G. inquinatus (Say)] appears to have a roughly linear bursa, with the spermathecal duct arising anteriorly. However, the illustrations of the bursa in Smith & Balsbaugh (1984) show that the origin of the spermathecal duct is various in Nearctic species of Glyphonyx. In most species, the spermathecal duct arises posteriorly, though the bursa is definitely not U-shaped. Some species, however, do have a recurved bursa with the spermathecal duct arising posteriorly (e.g., Smith & Balsbaugh, 1984, figs. 39, 44). I suspect that in Glyphonyx, the recurved shape of the bursa has been secondarily lost in most species; thus the bursa is linear, but the spermathecal duct arises posteriorly. The same appears to have occurred in Adrastus, in which the spermathecal duct arises about the center line of the bursa as it does in some species of Glyphonyx, and in Ctenoplus, Medonia, Parasilesis, Peripontius, Silesis and Synaptus in which bursa is linear but the spermathecal duct arises posteriorly as it does in most species of Glyphonyx.

Agriotes as defined by Becker (1956) presents special problems, since several states exist within this genus and Becker's definition is not accepted by all workers (Guryeva, 1972). The illustrations of Becker (1956) show that the bursa of Agriotes apicalis LeConte, A. bivittatus Van Dyke and A. criddlei is recurved with the spermathecal duct arising posteriorly. In A. thevenetii Horn and A. quebecensis Brown the spermathecal duct arises posteriorly

in a way that suggests the bursa is a reduced recurved type similar to Glyphonyx. In the rest of the species illustrated by Becker (1956), the spermathecal duct arises more or less anteriorly. In the type species of Agriotes (sensu stricto) and Agriotes (Ectinus), the bursa is roughly straight and the spermathecal duct arises anteriorly.

Armature of bursa copulatrix. In the Elaterini, the bursa is either unarmed; or bears spines which are generally distributed, or form bands or rows, or fan-like clusters; or bears spiny plates. Adrastus and the Sparsus group of Agriotes lack bursal spines or spiny plates. In some species, two states are combined. In at least one species of Aphanobius, the spines are arranged into multiple rows and fan-shaped clusters (at least eight clusters counted). In the type species of Neotrichophorus, the bursal spines are sparse, indistinct and arranged into three clusters (Fig. 11A). Most other taxa of the Elater group have the bursal spines generally distributed (Figs. 11B-D) or arranged into rows, but Elater decorus (Germar) has the fan-shaped cluster of spines characteristic of the following taxa, as well as a lateral band of spines. In Agelasinus, Ypsilostethus, some species of Agriotes, and the Pomachilius group, the bursal spines are clustered into a distinctive pair of dorsal-ventral fans of spines arising posteriorly, with or without a band of spines along the anterior margin of the bursa (see below) (Fig. 11E). The bases of the spines in the fans are fused to form discrete plates in some species, but the fan-shaped array of spines is always conspicuous and the spines are longer than the plate. In some species of Agriotes (sensu stricto) and Dalopius, and all species of Agriotes (Ectinus), most taxa of the Adrastus group, discrete spiny plates of various sizes and shapes are present (Figs. 11F-H). The spines on the plates are variously distinctive, but are shorter than the plate in most species and much sparser than in the fan-shaped clusters above. Bands of spines also may be present in addition to discrete spiny plates, e.g., Ctenoplus.

In those taxa with discrete bursal plates, the plates are either more or less rounded (Figs. 11F, H; Becker, 1956, figs. 6-15) in most taxa of the Agriotes group and some species of Dalopius, or more or less tear-drop shaped with an attenuated posterior end (Fig. 11G; Smith & Balsbaugh, 1984, figs. 33-50) in most taxa of the Adrastus group. The bursal plate is quite narrow and has little anterior curvature in Silesis, and thus less tear-drop shaped, but the posterior end is attenuated. The bursal plate is narrow and curved anteriorly in Ctenoplus, and appears intermediate between the condition in Silesis and the obviously tear-drop shaped bursal plates of the other

taxa.

The bursal armature in Agriotes is various and further study may show that the character states described above are not discrete. The bursa of the Sparsus group is unarmed, as mentioned above. The Criddlei group has the distinctive dorsal-ventral pair of fans of spines, while the Sputator group and Agriotes (Ectinus) have discrete spiny plates (Becker, 1956; Guryeva, 1979b). The shape of the spiny plate of A. apicalis (Becker, 1956, fig. 2), a member of subgenus Ectinus, is reminiscent of the tear-drop shaped plates of the Adrastus group, while the long marginal spines of the plates in Agriotes oblongicollis (Melsheimer), A. thevenetii Horn and A. opaculus (LeConte) (Becker, 1956, figs. 11, 13, 15, respectively), also members of subgenus Ectinus, suggest derivation from the fan-shaped clusters of spines.

Guryeva (1979b, figs. 584, 585, as Idolus) has illustrated the bursa copulatrix of Agriotella picipennis (Bach) and A. adrastoides (Reitter). Guryeva's illustrations show a fan of spines and two smaller clusters of uncertain shape for I. picipennnis, and three and possibly four fans of spines for I. adrastoides. Specimens of A. picipennis I have examined have a dorsal-ventral pair of fans of spines as well as two smaller fans of spines. Generic revision of Agriotella may show that the charcter states described here need to be further refined.

The presence of the anterior band of spines in those taxa with the dorsal-ventral pair of fans of spines (Fig. 11E) is not consistent within genera examined. The band is absent from the female syntype of Agelasinus viridis Candèze, but present in the unidentified species of Agelasinus from Argentina from which data were collected for the data matrix. The presence of the band of spines is various in Japanese species of Dalopius (Kishii, 1984, figs. 54-62). The length of the anterior band of spines is also various. In Pseudoderomecus fairmairei (Candèze), the band of spines extends posterad almost to the posterior end of the bursa, while in other taxa it is considerably shorter.

Accessory glands. In Sericus and Dolerosomus, the bursa copulatrix lacks an accessory gland. I am interpreting an accessory gland as any closed-end tube that enters the bursa copulatrix independently of the spermathecal duct. An accessory gland is absent from most genera of Elaterini. In Agriotes, Atractopterus, Old World species of Neotrichophorus (Fig. 11A), Orthostethus and Parallelostethus (Fig. 11C), one accessory gland is present; this state may also be present in Chiagosnius. In

Aphanobius and Elater (Fig. 11D), two accessory glands are present.

Colleterial glands. In most genera of Elaterini, the colleterial glands are elongate and semi-stalked (Fig. 11A), but in a few, e.g, Atractopterus, Elater, Orthostethus and Parallelostethus (Fig. 11C), the colleterial glands are globular with a wide base along the vagina.

The characters presented above are those I examined in preparation for phylogenetic analysis. I have presented them in part as an explicit statement of which character states I examined, and to suggest possible candidates for further evaluation in generic revisions.

CLASSIFICATION OF THE ELATERINI

The classification presented below is based on the hypothesized reconstructed phylogeny. Taxa are arranged in the order in which they appear in Fig. 12. Species marked with an asterisk (*) were examined in detail as discussed in the Methods section. I treat all genera listed below as valid despite evidence to the contrary. In the interests of nomenclatural stability, I do not feel changes other than removing Atractopterus from synonymy with Sericus are appropriate for these taxa without further study.

Tribe Elaterini Leach

Elaterini Leach, 1815: 384. Type genus: Elater Linnaeus.

Agriotites Castelnau, 1840:233. Type genus: Agriotes Eschscholtz. NEW SYNONYM.

Pomachiliites Candèze, 1860:1. Type genus: Pomachilius Eschscholtz. NEW SYNONYM.

Ludiites Candèze, 1863:2, 281. Type genus: Ludius Berthold; isogenotypic synonym of Elater.

Adrastites Candèze, 1863:448. Type genus: Adrastus Eschscholtz. NEW SYNONYM.

Steatoderini Schwarz, 1906:5, 252. Type genus: Steatoderus Dejean; isogenotypic synonym of Elater.

Synaptina Jakobson, 1913:734. Type genus: Synaptus Eschscholtz. Synonymized with Adrastinae by Fleutiaux, 1940c:19.

NOTES ABOUT SYNONYMY

A family group name based on Agriotes is traditionally credited to Champion (1896:511). However, the use of Agriotites by Castelnau (1840) seems to satisfy the criteria of valid publication specified by the Code of Zoological Nomenclature (International Trust for Zoological Nomenclature, 1985).

DIAGNOSIS: Pronotum with emarginate anterior subpronotal lobe, lobe lightly (Fig. 4F) or heavily (Fig. 4I) sclerotized, notch shallow (Fig. 4H) or deep (Fig. 4I); ventral margin of gena diverging from ventral margin of eye (Fig. 1C); genal projection relatively long (Fig. 1C), extended anterad ventral condyle of mandible, ventral margin of gena unicarinate at apex (Fig. 1C); ventral

condyle of mandible situated more anterad than dorsal condyle (Fig. 3B).

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: I recognize 35 described genera in this tribe, collectively distributed in North, Central and South America, Eurasia southeast to New Guinea, New Zealand; possibly also Australia and central and southeastern Africa but I have not seen any specimens I am assigning to this tribe from these areas. The tribe contains at least 800 described species.

RELATIONSHIPS: The Elaterini are the sister group to the Sericosomini, a group that is not necessarily monophyletic. The Elaterini and Sericosomini are distinguished from all other Elaterinae by having the genal margin divergent anteriorly from the ventral margin of the eye, rather than being subparallel as in other Elaterinae.

STATUS: From Fig. 12, I conclude that the traditional Elaterini and the Pomachiliini sensu Guryeva (1979b) are not sister groups. Rather, the traditional Pomachiliini are relatively more derived members of the Elaterini, with Agelasinus and Ypsilostethus having character combinations that bridge the gap between the two traditional tribes. The Pomachiliini sensu Guryeva (1979b) encompass taxa 13-30 in Fig. 12. The evolution of the distinctive fans of spines on the bursa copulatrix (Fig. 11E), found in all species of the Pomachilius group (taxa 13, 14, 16-23 in Fig. 12), occurs in Ancestor I. The heavily sclerotized and deeply notched subpronotal lobe of the prothorax (Fig. 4I), found in all taxa of the Pomachilius, Agriotes and Adrastus groups (taxa 13-30 in Fig. 12) first appears in Ancestor J. In my opinion, the sequential appearance of these two character states in relatively derived taxa of the Elater group (taxa 1-12 in Fig. 12) effectively renders the distinction between the traditional Elaterini and the Pomachiliini sensu Guryeva (1979b) arbitrary. The Elaterini cannot be defined as monophyletic without including the traditional tribes Pomachiliini, Agriotini and Adrastini, since this would require excluding over half of the descendents of the common ancestor. For this reason, I have synonymized the tribal names Pomachiliini, Agriotini and Adrastini with the Elaterini.

KEY TO GENERA OF ELATERINI

The following key is presented with the full knowledge that it is more likely to reveal problems than solve them. The large contingent of Neotropical taxa keying out after couplet 23, and the New World species of Neotrichophorus, are likely to cause the most problems. See classification

that follows for details.

1. Margins of mesosternal fossa raised and beaded anterad mesocoxae (Fig. 7D) 16
1' Margins of mesosternal fossa raised or not, not beaded (Fig. 7C) 2

2(1'). Head with complete frontal carina (Fig. 1D) 3
2' Frontal carina incomplete: supraantennal crests not meeting (Fig. 1G) 5

3(2). Tarsal claws flanged (Fig. 10F); Neotropical Region ..... 12. Ypsilostethus Candèze
3' Tarsal claws simple (Fig. 10E) 4

4(3'). Pronotum much longer than wide; hypomeron not grooved laterally; size larger (10-12 mm); California ..... 6. Leptoschema Horn
4' Pronotum about as long as wide; hypomeron grooved ventrad lateral carina of pronotum; size smaller (2-3 mm); New Zealand, England ..... 33. Panspoeus Sharp

5(2'). Prosternal mucro steeply sloped dorsally (Fig. 6E); Neotropical Region ..... 11. Agelasinus Candèze
5' Prosternal mucro at best gently sloped dorsally (Fig. 6B) 6

6(5'). Margins of mesosternal fossa relatively thick, subparallel, raised from posterior end of mesosternum to anterior articulating surfaces (Figs. 7H, 8F); eastern North America, eastern Asia ..... 9. Parallelostethus Schwarz
6' Margins of mesosternal fossa either not raised from posterior margin to anterior articulating surface, or divergent anterad mesocoxae, or relatively thinner (Figs. 8A-E) 7

7(6'). Mesosternum almost perpendicular at level of anterior margin of mesocoxae, horizontal between mesocoxae (Fig. 7E); southern Nearctic, northern Neotropical Regions ..... 7. Orthostethus Lacordaire
7' Mesosternum gently sloped anterad mesocoxae 8

8(7'). Prosternal mucro with abrupt perpendicular declivity between procoxae and subapical tooth (Fig. 6C); southern Nearctic, northern Neotropical Regions ..... 4. Diplostethus Schwarz
8' Ventral surface of prosternal mucro convex, horizontal or gradually sloping dorsally between procoxae and subapical/apical tooth (Figs. 6A, B, D) 9

9(8'). Mesepimeron with distinct anterolateral projection (Fig. 8G) 10
9' Mesepimeron without anterolateral projection (Fig. 8H); eastern and western North America, Japan .... 5. Atractopterus LeConte

10(9). Metacoxal plate with distinct tooth at level of trochanter-femur joint (Fig. 9F) 13
10' Metacoxal plate only slightly enlarged at level of trochanter-femur joint (Fig. 9G) 11

11(10'). Tarsomeres without lobes (as in Fig. 10A) 12
11' Tarsomere 4 with small ventral lobe; Middle East ..... 34. Pseudagriotes Schwarz

12(11). Prosternal mucro with subapical tooth near mid-point (Fig. 6D); Europe ... 3. Pittonotus Kiesenwetter
12' Prosternal mucro with subapical tooth closer to apex (Fig. 6B); southern Nearctic, northern Neotropical Regions ... 2. some New World Neotrichophorus Jakobson

13(10). Prosternal mucro with ventral tooth subapical (Fig. 6B) 14
13' Prosternal mucro with ventral tooth apical (Fig. 6A) 15

14(13). Anterior articulating surface of mesosternum restricted to anterior surface (Fig. 8C); Neotropical Region ..... 10. Probothrium Candèze, 2. some New World Neotrichophorus Jakobson
14' Anterior articulating surface of mesosternum occupying part of ventral surface; distribution uncertain: at least Europe, eastern North America 8. Elater Linnaeus

15(13'). Prosternal mucro horizontal from procoxae to apical tooth (Fig. 6A); eastern Asia .... 1. Aphanobius Eschscholtz
15' Prosternal mucro gradually declivous from procoxae to apical tooth (as in Fig. 6B); southern Europe, Asia ..... 2. Old World Neotrichophorus Jakobson

16(1). Tarsal claws pectinate (Fig. 10G) 17
16' Tarsal claws simple (Fig. 10E) 23

17(16). Two circular, steep-sided periocular pits present (Figs. 1E, I) 18
17' Periocular pits either absent (Fig. 1H), or irregular in shape (Fig. 1J) 22

18(17). Supraantennal crests separated along anterior margin of frons by at least half length of labrum . 19
18' Supraantennal crests various, either joined in form of complete frontal carina with carina separated from

anterior margin of frons (Fig. 1E) or not, or supraantennal crests meeting anterior margin of frons but separated by less than one-quarter length of labrum; Nearctic, Neotropical Regions, eastern Asia, Africa ..... 29. Glyphonyx Candèze

19(18). Tarsomere 3 lobed, tarsomere 4 simple (as in Fig. 10B); Europe, southeast Asia 25. Synaptus Eschscholtz
19' Tarsomere 3 simple, tarsomere 4 lobed (as in Fig. 10C) 20

20(19'). Prosternal mucro with subapical tooth tridentate (Fig. 6F); eastern Asia ..... 26. Parasilesis Ohira
20' Prosternal mucro with subapical tooth unidentate (Figs. 6G, H) 21

21(20'). Ventral surface of prosternal mucro as wide as dorsal surface (Fig. 6G); Asia ... 30. Silesis Candèze
21' Ventral surface of prosternal mucro narrower than dorsal surface (Fig. 6H); Europe .... 28. Peripontius Guryeva

22(17). Periocular pits present, irregular in shape (Fig. 1J); longitudinal metasternal suture absent (as in Fig. 9C); margins of mesosternal fossa distinctly raised and thickened between mesocoxae (Fig. 7F); southeast Asia ..... 27. Ctenoplus Candèze
22' Periocular pit absent (Fig. 1H); longitudinal metasternal suture present (as in Fig. 9A); margins of mesosternal fossa only slightly raised, not thickened between mesocoxae (Fig. 7G); Europe .... 24. Adrastus Eschscholtz

23(16'). Lateral carina of pronotum joined to anterior margin of pronotum at or very near to same point as mesal margin of hypomeron (Fig. 5B) 26
23' Lateral carina of pronotum and mesal margin of hypomeron distinctly separated at anterior margin (Fig. 5D) 24

24(23'). Tarsomeres unlobed (as in Fig. 10A); frontal carina incomplete (as in Fig. 1G) 25
24' Tarsomere 4 lobed ventrally (as in Fig. 10C); frontal carina complete; Chile . 20. Pseudoderomecus Fleutiaux

25(24). Metasternum with lateral submarginal groove (as in Fig. 9E); Neotropical Region .... 13. Mesembria Arnett
25' Metasternum without lateral submarginal groove (Fig. 9D); Nearctic, Palaearctic Regions .... 14. Dalopius Eschscholtz

26(23). Tarsomeres simple (as in Fig. 10A) 27

26' Tarsomere 3 or 4 lobed ventrally (as in Figs. 10B, C) 30

27(26). Frontal carina complete (Figs. 1D, F) 28
27' Supraantennal crests separate (as in Fig. 1G); Nearctic, Neotropical, Palaearctic, Oriental Regions ..... 15. Agriotes Eschscholtz (sensu lato), 32. Insuliectinus Kishii, 31. Chatanayus Fleutiaux

28(27). Metasternum with lateral submarginal groove (Fig. 9E); Neotropical Region ..... 18. Deromecus Solier
28' Metasternum without lateral submarginal groove (as in Fig. 9D) 29

29(28'). North America, Europe ..... 16. Agriotella Brown
29' South America ..... 17. Cosmesus Eschscholtz

30(26'). Tarsomere 3 lobed ventrally; tarsomere 4 simple; lateral carina of pronotum complete 31
30' Tarsomere 3 simple; tarsomere 4 lobed ventrally; lateral carina of pronotum incomplete; Chile ..... 19. Medonia Candèze

31(30). Frontal carina complete, almost horizontal between eyes, clearly raised above anterior margin of frons (Fig. 1D) 32
31' Frontal carina various; if frontal carina complete, carina also curved toward and usually contiguous with anterior margin of frons (Fig. 1F); Neotropical Region ..... 22. Paracosmesus Schwarz

32(31). Anterior and posterior distal angles of antennomeres produced; Neotropical Region ..... 35. Smilicerus Candèze
32' Only posterior distal margin of antennomeres produced 33

33(32'). Mesotrochantin about as long as median width (as in Fig. 8D); Europe ..... 21. Betarmon Kiesenwetter
33' Mesotrochantin concealed (as in Fig. 8A); Neotropical Region ..... 23. Pomachilius Eschscholtz

1. Genus Aphanobius Eschscholtz

Aphanobius Eschscholtz, 1829:33. Type species: Aphanobius longicollis Eschscholtz (designated by Candèze, 1863:322).

DIAGNOSIS: Frontal carina incomplete; right mandible without conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro horizontal from procoxae to apex, ventral tooth apical (Fig. 6A); mesosternum gradually sloped between mesocoxae, margins of mesosternal fossa not raised and beaded; lateral lobes of mesosternum with conspicuous depression anteriorly, anterior articulating surface on anterior surface only (Fig. 8E); mesepimeron with anterolateral projection; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate toothed at level of trochanter-femur joint, tarsomeres and tarsal claws simple; bursa copulatrix roughly linear, with spines aligned in multiple rows and fans or not.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Oriental, Afrotropical Regions. Schenkling (1927) lists 13 species from eastern Asia, distributed collectively from Palaearctic Japan to Oriental India and east to the Philippine archipelago and Java in the Indo-Australian archipelago, and eight species from Afrotropical eastern Africa, living in Mauritius, Madagascar and coastal Tanzania.

RELATIONSHIPS: Sister group of Old World species of Neotrichophorus + (Pittonotus + (Diplostethus + New World species of Neotrichophorus)) (Fig. 12).

WAY OF LIFE: Little seems to be known about the life history or habits of the species of Aphanobius. Five of the six specimens of A. longicollis I collected in Thailand were attracted to ultraviolet light; the sixth was collected from plants in a pine forest. All were collected below 1300m elevation.

MATERIAL EXAMINED: A. alaomorphus Candèze* (3), A. sp. near malaccensis Candèze (2), A. longicollis Eschscholtz (6).

STATUS: The genus has not been revised, and has not been shown to be monophyletic.

2. Genus Neotrichophorus Jakobson

Neotrichophorus Jakobson, 1913:742; new name for Trichophorus Mulsant & Godart, 1853, preoccupied by Trichophorus Serville, 1834 (Cerambycidae). Type species: Trichophorus guillebelli Mulsant & Godart (by monotypy).

Genomecus Solier, 1851:29. Type species: Genomecus ruficollis Solier (by monotypy).

Amblygnathus Solier, 1851:39. Type species Amblygnathus abdominalis Solier (by monotypy). Preoccupied by Amblygnathus Dejean, 1829 (Carabidae).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively small (Fig. 3C), and mandible with distinct crest between apicolateral groove and ventral margin in some New World species (Fig. 4A); basistipes of maxilla with more than one long seta (Fig. 4D); anterior subpronotal lobe relatively lightly sclerotized with shallow notch (Fig. 4G); lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro gradually sloping dorsally posterad procoxae (Fig. 6B), ventral tooth apical in Old World species, apical or subapical (Fig. 6B) in New World species; mesosternum gradually sloped between mesocoxae, margins of fossa not raised and beaded (Fig. 7C), anterior articulating surface on anterior surface only (Figs. 8B,C); lateral lobes of mesosternum with subcircular mesolateral depression bounded posteriorly by sharp ridge in Old World species (Fig. 8B), unmodified in New World species (Fig. 8C); mesepimeron with anterolateral projection (Fig. 8G); mesotrochantin ca. twice as long as median width in ventral aspect (Figs. 8B, C); metacoxal plate toothed at level of trochanter-femur joint in Old World species, toothed or only slightly enlarged (Fig. 9G) in New World species; tarsomeres and tarsal claws simple; bursa copulatrix roughly linear in Old World species (Fig. 11A), distinctly coiled in at least some New World species (Fig. 11B), spines variously distributed.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Oriental, Nearctic, Neotropical Regions. Schenkling (1927) and Fleutiaux (1936) list 25 Old World species of Neotrichophorus (including the type species), distributed collectively from Palaearctic central Europe east to Japan and south to Oriental India and Java in the Indo-Australian archipelago. Roache (1961) lists five species for Nearctic southern United States and northern Mexico. At least two of the species of Ludius [a junior synonym of Elater]

described by Champion (1896) from Central America (depressus and physorhinus) belong in Neotrichophorus. Schenkling (1927) lists one species from Brazil.

RELATIONSHIPS: Not monophyletic. Old World species are the sister group of Pittonotus + (Diplostethus + New World species of Neotrichophorus) (Fig. 12).

WAY OF LIFE: Little is known about the life history or habits of any species of Neotrichophorus. Adults of at least the New World species are attracted to lights. I have collected specimens of N. depressus (Champion) on understory shrubs at night in Costa Rica. Adults of N. guillebeaui in France and Italy are crepuscular, and have been collected by sweeping vegetation and at lights; the larva is not known (Leseigneur, 1972; Platia & Bartolozzi, 1988). In Thailand, I collected adults of N. hirtellus (Candèze) on understory plants both during the day and at night, and adults of N. rugosus (Fleutiaux) on understory plants during the day and in malaise traps.

MATERIAL EXAMINED: Old World species: N. guillebeaui (Mulsant)* (3), N. erubescens (Candèze) (1), N. hirsutus (Candèze) (1), N. hirtellus (Candèze) (3), N. junior (Candèze) (3), N. sp. near suturalis (Candèze) (1), N. rugosus (Fleutiaux) (5). New World species: N. carolinensis (Schaeffer)* (42), N. arizonicus (Schaeffer)* (15), N. substriatus (Schaeffer) (4), N. depressus (Champion)* (20), N. texanus (Schaeffer) (1), N. variolatus (Schaeffer) (1), N. physorhinus (Candèze) (1), N. decorus (Germar) (8), N. ruficollis (Solier)* (16).

STATUS: This genus requires revision. The distinction between Neotrichophorus and Probothrium requires critical study (see Probothrium). The New World species are not a monophyletic group. The Mesoamerican N. depressus and Chilean N. decorus share few derived characters with the southern Nearctic species used in the data matrix.

Technically, Genomecus Solier has priority over Neotrichophorus Jakobson. Specimens of the type species of Genomecus will key to Probothrium/some New World Neotrichophorus (couplet 14) in my key. Since I do not believe Neotrichophorus is monophyletic, I retain the traditional synonymies in the interests of nomenclatural stability pending a revision of this genus.

3. Genus Pittonotus Kiesenwetter

Pittonotus Kiesenwetter 1859:19. Type species: Elater theseus Germar (by monotypy).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro with ventral tooth at midpoint (Fig. 6D); mesosternum gradually sloped between mesocoxae, margins of fossa not raised and beaded, anterior articulating surface on ventral surface; mesepimeron with anterolateral projection; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate only slightly enlarged at level of trochanter-femur joint; tarsomeres and tarsal claws simple; bursa copulatrix roughly linear, spines more or less uniformly distributed.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The genus contains two species (Platia & Marini, 1990) living in southern Europe and the Middle East.

RELATIONSHIPS: Sister group of Diplostethus + New World species of Neotrichophorus (Fig. 12).

WAY OF LIFE: Little seems to be known about the life history or habits of these species. Adults of P. theseus have been collected by beating shrubs (Leseigneur, 1972).

MATERIAL EXAMINED: P. theseus (Germar)* (3).

STATUS: Platia and Marini (1990) provide a diagnosis of the two species they recognize in this genus.

4. Genus Diplostethus Schwarz

Diplostethus Schwarz, 1907:252, 258. Type species: Aphanobius setosus Germar (designated by Hyslop, 1921: 640).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, and with distinct crest between apicolateral groove and ventral margin, terebral tooth of right mandible relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch (Fig. 4H); lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron (Fig. 5E); prosternal mucro with almost perpendicular declivity between procoxae and subapical tooth (Fig. 6C); mesosternum gradually sloped between mesocoxae, margins of fossa not raised and beaded, anterior articulating surface on anterior surface only; mesepimeron with anterolateral projection; mesotrochantin ca. twice as

long as median width in ventral aspect; tarsomeres and tarsal claws simple; bursa copulatrix distinctly coiled, spines more or less uniformly distributed.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical and Nearctic Regions. There are four described species in Diplostethus, ranging collectively from southern Nearctic Arizona to northern Neotropical Venezuela.

RELATIONSHIPS: Sister group of some New World species of Neotrichophorus (Fig. 12).

WAY OF LIFE: Little is known about the life history and habits of the species of Diplostethus. Adults are attracted to lights. The lightly sclerotized ovipositor suggests eggs are deposited in relatively soft substrates such as friable soil or leaf litter.

MATERIAL EXAMINED: D. setosus (Germar) (13), D. opacicollis Schaeffer* (90), D. peninsularis (Champion) (20).

STATUS: The genus has not been revised, and thus has not been shown to be monophyletic. Ludius candezei Lewis nec Fauvel, listed under Diplostethus by Schenkling (1927) is now placed in Parallelostethus, as P. georgelewisi Suzuki (Kishii, 1987).

5. Genus Atractopterus LeConte

Atractopterus LeConte, 1853:454. Type species: Atractopterus fusiformis LeConte (=Elater honestus Randall) (designated by Hyslop, 1921:630).

DIAGNOSIS: Frontal carina incomplete; right mandible without conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch (Fig. 4F); lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; mesosternum gradually sloped anterad mesocoxae, margins of fossa divergent, not raised and beaded, anterior articulating surface on ventral surface; mesepimeron without anterolateral projection (Fig. 8H), setae arising on tubercles (Fig. 8H); mesotrochantin ca. twice as long as median width in ventral aspect; tarsomeres and tarsal claws simple; bursa copulatrix roughly linear, spines arranged in rows.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic, Palaearctic Regions. I include three species in this genus: A. honestus (Randall) from Nearctic eastern North

America, A. rugosus (Van Dyke) from California, and A. sericarius (Motschulsky) from Palaearctic Japan. All of these names are NEW COMBINATIONS.

RELATIONSHIPS: Unresolved. Atractopterus forms a polychotomy with Leptoschema, Orthostethus, Elater + Parallelostethus and the ancestor of Probothrium et al. (Fig. 12; see also Figs. 13, 14).

WAY OF LIFE: Nothing is known about the life history or habits of the species of Atractopterus.

MATERIAL EXAMINED: A. honestus (Randall)* (4), A. rugosus (Van Dyke) (1), A. sericarius (Motschulsky) (1)

STATUS: Atractopterus is here removed from synonomy with Sericus and is used as the generic name for the three species listed above. All these species appear to be rare in collections, and little is known about them. A. rugosus and A. sericarius are included based on specimens identified as such in the collection of the California Academy of Sciences.

6. Genus Leptoschema Horn

Leptoschema Horn, 1884:50. Type species: Agriotes protractus Horn (by original designation).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; right mandible without conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; pronotum much longer than wide; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; prosternal mucro horizontal posterad procoxae; margins of mesosternal fossa not raised and beaded, anterior articulating surface on anterior surface only; mesotrochantin ca. twice as long as median width in ventral aspect; tarsomeres and tarsal claws simple.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic Region. This genus contains two described species, both of which are recorded only from California (Stibick, 1970).

RELATIONSHIPS: Unresolved. See Atractopterus.

WAY OF LIFE: Nothing is known about the life history or habits of the species of Leptoschema.

MATERIAL EXAMINED: L. protractum (Horn) (3), L.

praelontactum Stibick (1).

STATUS: The genus has been revised by Stibick (1970), who placed it in the traditional Pomachiliini.

7. Genus Orthostethus Lacordaire

Orthostethus Lacordaire, 1857:217. Type species: Aphanobius infuscatus Germar (by original designation).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, and with distinct crest between apicolateral groove and ventral margin, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro horizontal posterad procoxae; mesosternum almost perpendicular at level of anterior margin of mesocoxae and horizontal between mesocoxae (Fig. 7E), margins of fossa not beaded, anterior articulating surface on anterior surface only; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate toothed at level of trochanter-femur joint (Fig. 9F); tarsomeres and tarsal claws simple; bursa copulatrix roughly linear, accessory gland arising near midline from coiled enlargement of bursa, spines more or less uniformly distributed.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic and Neotropical Regions. The collective range of the nine described species extends from the Nearctic southern United States to Neotropical Colombia (Schenkling, 1927).

RELATIONSHIPS: Unresolved. See Atractopterus.

WAY OF LIFE: Adults of Orthostethus are attracted to lights. Savely (1939) reports large larvae of O. infuscatus (Germar) in southeastern United States were found in pine logs that had been dead for more than three years, and that the larvae are apparently wood feeders.

MATERIAL EXAMINED: O. infuscatus (Germar)* (30), O. piceus Candèze (2), O. caviceps Schaeffer (1), unidentified species from Mexico (2) and Ecuador (1).

STATUS: Orthostethus has not been revised and the monophyly of this genus is unproven.

8. Genus Elater Linnaeus

Elater Linnaeus, 1758:404. Type species: Elater ferrugineus

Linnaeus (designated by Latreille, 1810:426).

Ludius Berthold, 1827:336. Type species: Elater ferrugineus Linnaeus (by monotypy). Isogenotypic with Elater.

Steatoderus Dejean, 1833:94. Type species: Elater ferrugineus Linnaeus (by monotypy). Isogenotypic with Elater.

Nipponoelater Kishii, 1985:23. Type species: Elater sieboldi Candèze (by original designation). Described as subgenus of Elater.

DIAGNOSIS: Frontal carina incomplete; right mandible without conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro horizontal posterad procoxae, ventral tooth either near apex (subgenus Elater) or near midpoint (subgenus Nipponoelater); mesosternum gradually sloped between mesocoxae, margins of fossa not raised and beaded, anterior excavation of mesosternum either restricted to anterior surface (subgenus Nipponoelater) or occupying part of ventral surface (subgenus Elater); mesepimeron with anterolateral projection; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate toothed at level of trochanter-femur joint, tarsomeres and tarsal claws simple; bursa copulatrix with spermathecal duct and an accessory gland arising from enlargement near midline, spines more or less uniformly distributed (Fig. 11D).

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Nearctic, Oriental, Afrotropical, Neotropical Regions. Schenkling (1927) lists species from the biogeographical areas listed above, but this includes species now assigned to several other genera. The type species of Elater occurs in Europe. Some Japanese species are assigned to subgenera other than Elater (Kishii, 1987), and may not be congeneric with E. ferrugineus. Roache (1961) lists four North American species, one in eastern North America and three in the southwestern United States. Lane (1971) transfers two species from the western United States previously included in Megapenthes to Elater. Schenkling (1927) lists 20 Central and South American species under Ludius, an isogenotypic synonym of Elater. One of the species of Ludius listed by Schenkling (1927) is the type species of Diplostethus; the remainder are placed by Blackwelder (1944) in Crigmus LeConte, along with species now included

in Neotrichophorus (for the status of Crigmus, see Probothrium). Schenkling (1927) lists five species from central Africa, seven species from Australia and New Guinea, and 17 species from southeast Asia. The status of this latter group must be considered suspect pending further study; at least three species (erubescens Candèze from New Guinea, and bonifacyi (Fleutiaux) and rugosus (Fleutiaux) from Vietnam) belong in Neotrichophorus.

RELATIONSHIPS: Sister group of Parallelostethus (Fig. 12).

WAY OF LIFE: Larvae of E. abruptus Say live in rotten wood of deciduous trees in eastern United States, apparently are neither predaceous nor cannibalistic, and pupate in spring or early summer (Jewett, 1946, as Neotrichophorus). Adults of the same species are attracted to fermenting baits (Champlain & Knull, 1932). Larvae of the European E. ferrugineus also live in rotten wood, especially in tree holes of Quercus, Fagus, Salix and Aesculus. The species is reported to be polyphagous, and larvae attack larvae and pupae of scarabaeids and other beetles in the same habitat. Under artificial conditions, larvae require two to three years to mature. Pupation occurs in May and June and adults appear in July and August. Adults are crepuscular and are attracted to lights and liquid traps in tree holes. This species has been found at elevations up to 1500m in France (Iablokoff, 1943; Leseigneur, 1972; Palm, 1972).

MATERIAL EXAMINED: E. ferrugineus Linnaeus* (2), E. abruptus Say* (3), E. tartareus LeConte (4), E. nipponensis (Lewis) (1), E. (Nipponelater) sieboldi (Candèze) (2), E. (Nipponelater) babai Suzuki (1), unidentified species of Elater (Nipponelater) from Malaysia (1). I have also examined specimens of E. ater (Candèze) and E. lecontei (Horn) in the collection of the California Academy of Sciences, but I am not convinced they belong in the Elaterini. Further study of the latter two taxa is required.

STATUS: As indicated above, the genus as currently defined is not monophyletic, and is in need of revision.

Lane (1971) transferred E. tartareus and E. nigriventris LeConte to Elater from Megapenthes, but Becker (1971) included them in Megapenthes. Specimens I have examined of E. tartareus, although superficially similar to Megapenthes aterrimus (Motschulsky), have the same type of gena as other Elaterini. Further study may prove this species is more closely related to Neotrichophorus than to Elater. I have not seen specimens of E. nigriventris.

9. Genus Parallelostethus Schwarz

Parallelostethus Schwarz, 1907:258. Type species: Elater attenuatus Say (designated by Hyslop, 1921:662).

DIAGNOSIS: Frontal carina incomplete; right mandible without conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro horizontal posterad procoxae; margins of mesosternal fossa parallel, raised anterad mesocoxae but not beaded (Figs. 7H, 8F), anterior articulating surface on anterior surface only; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate toothed at level of trochanter-femur joint; tarsomeres and tarsal claws simple; bursa copulatrix roughly linear, accessory gland arising near midline from enlargement of bursa, spines more or less uniformly distributed (Fig. 11C).

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic, Palaearctic Regions. Schenkling (1927) lists seven species of Parallelostethus. The type species lives in Nearctic eastern North America. The remaining six species live in eastern Asia, collectively distributed from Palaearctic China and Japan to Oriental Sri Lanka and east to the Philippine archipelago and Sulawesi, in the Indo-Australian archipelago (Schenkling, 1927; Kishii, 1987).

RELATIONSHIPS: Sister group of Elater.

WAY OF LIFE: Larvae of P. attenuatus (Say) live in rotten wood of deciduous trees in the eastern United States, apparently are neither predaceous nor cannibalistic, and pupate in spring or early summer (Jewett, 1946). Kirk (1922) reports that larvae of the same species eat decaying wood, though Dietrich (1945) reports some larvae were collected in well drained muck soils. Adults are attracted to fermenting baits in July and August (Champlain & Knull, 1932).

MATERIAL EXAMINED: P. attenuatus (Say)* (4), P. acutus (Candèze) (6), P. rubiginosus (Candèze) (1), P. georgelewisi Suzuki (1).

STATUS: Based on character states currently considered generically significant, Parallelostethus is not monophyletic. P. attenuatus has the mesal margin of the hypomeron punctate, while at least two of the species from eastern Asia have the mesal margin of the hypomeron

impunctate. Such a difference traditionally is considered sufficient for recognizing two genera.

Kishii (1987), following Ohira (1960), treats Parallelostethus as a subgenus of Elater.

10. Genus Probothrium Candèze

Probothrium Candèze, 1863:287. Type species: Probothrium pupillum Candèze (designated by Hyslop, 1921:666).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively small; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; prosternal mucro gently sloping dorsally posterad procoxae, ventral tooth subapical; mesosternum almost perpendicular between mesocoxae, margins of fossa not raised and beaded, anterior articulating surface on anterior surface only; mesepimeron with anterolateral projection; mesotrochantin ca. twice as long as median width in ventral aspect; metacoxal plate toothed at level of trochanter-femur joint; tarsomeres and tarsal claws simple; bursa copulatrix recurved, spermathecal duct arising posteriorly, spines more or less uniformly distributed.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. At least 13 species of Probothrium are recognized (Schenkling, 1927), collectively ranging from Mexico to Argentina and Peru.

RELATIONSHIPS: Sister group of Agelasinus et al. (Fig. 12)

WAY OF LIFE: Little is known about the life history or habits of the species in this genus. One species has been reared from a larva collected in a decayed log in southern Brazil; pupation required about two weeks (Costa & Casari-Chen, 1984).

MATERIAL EXAMINED: P. amplicolle Candèze (3), P. pubescens (Kirby) (6), P. velutinum (Germar)* (4), P. sp. near velutinum (1), P. rufivellum Candèze (3), unidentified species from Paraguay (3).

STATUS: The monophyly of this genus is unproven. The almost perpendicular posterior margin of the mesosternum is traditionally considered diagnostic of Probothrium. However, this character state may grade into the gradually

sloping posterior margin of Neotrichophorus. I have found some species difficult to assign to one genus or the other on the basis of this character. Further study is required.

Crigmus LeConte, 1853:453 and Probothrium may be synonyms. LeConte named Elater hepaticus Germar as the type species of Crigmus, but apparently misidentified the species. Elater hepaticus LeConte, not Germar, is now Neotrichophorus carolinensis (Schaeffer) (Schaeffer, 1916; Lane, 1948). For this reason, North American authors have regarded Crigmus and Neotrichophorus as synonyms, or included in Crigmus species previously or currently placed in Neotrichophorus (e.g., Blackwelder, 1944). However, the species LeConte intended as the type species is not relevant - the species he named is Elater hepaticus Germar. The true identity of E. hepaticus is disputed. Champion (1896:506), who claims to have seen the type material, placed E. hepaticus in Probothrium, "very nearly allied to P. rufivellum Cand." If this is correct, Crigmus is the senior synonym of Probothrium. Champion's actions have not been accepted by other workers. Schwarz (1907) placed E. hepaticus in Orthostethus. Schenkling (1927), who does not cite Champion's reference to E. hepaticus, follows Schwarz (1907), and restricts the distribution of E. hepaticus to the southern United States. Blackwelder (1944), who largely follows Schenkling (1927), does not list E. hepaticus in his checklist of Neotropical beetles.

Champion (1896:506) described the mesosternum between the mesocoxae as "nearly vertical" and the metacoxal plates as "the acutely, triangularly dilated posterior coxal plates". Both of these character states are present in Probothrium, though the description of the latter is subject to interpretation. I interpret it as meaning toothed at the trochanter-femur joint as I have described the character state. The metacoxal plate in Orthostethus is toothed at the trochanter-femur joint as well, but the mesosternum is nearly vertical at the level of the anterior margin of the mesocoxal cavities rather than between them. I have not seen the type material of E. hepaticus. Since Crigmus would have priority over Probothrium, in the interests of nomenclatural stability I defer judgement on this matter until the identity of Elater hepaticus Germar can be established.

11. Genus Agelasinus Candèze

Agelasinus Candèze, 1863:335. Type species: Agelasinus viridis Candèze (designated by Hyslop, 1921:624).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively

large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively lightly sclerotized with shallow notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron (Fig. 5F); prosternal mucro steeply sloping dorsally posterad procoxae (Fig. 6E); margins of fossa not raised and beaded, anterior articulating surface on ventral surface; mesepimeron with anterolateral projection; mesotrochantin ca. twice as long as median width in ventral aspect; tarsomeres and tarsal claws simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The seven described species range collectively from Colombia in the north to Peru in the south. Data for phylogenetic analysis were taken from an unidentified species from Argentina. I have also seen specimens of this genus from Costa Rica.

RELATIONSHIPS: Sister group of (Ypsilostethus + Mesembria) et al. (Fig. 12).

WAY OF LIFE: Little is known about the habits or life history of the species in this genus. The specimens from Costa Rica were collected at 1500m in February. Those from Argentina were collected in Nothofagus forest in December.

MATERIAL EXAMINED: A. viridis Candèze, type series (1 male, 1 female), unidentified species from Costa Rica (4), Venezuela (3) and Argentina* (4).

STATUS: Agelasinus has not been revised. The monophyly of the included species is unproven.

12. Genus Ypsilostethus Candèze

Ypsilostethus Candèze, 1859:521. Type species: Ypsilostethus semiotulus Candèze (by monotypy).

DIAGNOSIS: Frontal carina complete, horizontal, narrowly separated from anterior margin of frons; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with more than one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; margins of fossa raised between mesocoxae but not beaded, anterior articulating surface on ventral surface; lateral lobes of mesosternum with subreniform mesolateral depression; mesepimeron with anterolateral projection; mesotrochantin ca. as long as

median width in ventral aspect; tarsomeres simple, tarsal claws flanged (Fig. 10F); bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines (Fig. 11E).

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The genus is monobasic. The only species lives in Colombia, Venezuela and Costa Rica.

RELATIONSHIPS: Possibly the sister group of Mesembria (Fig. 12); see discussion in Evolutionary Considerations.

WAY OF LIFE: Nothing is known about the life history or habits of Y. semiotulus. Adults have been taken in malaise traps.

MATERIAL EXAMINED: Y. semiotulus Candèze* (5).

STATUS: Ypsilostethus is here transfered from the Megapenthini (Elaterinae). The configuration of the gena, subpronotal lobe and fan-shaped clusters of spines on the bursa copulatrix place this genus in the Elaterini.

13. Genus Mesembria Arnett

Mesembria Arnett, 1955:601. Type species: Cosmesus subtilis Candèze (by original designation).

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove; basistipes of maxilla with only one long seta; lateral carina of pronotum joining anterior margin of pronotum dorsad mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; lateral lobes of mesosternum with subreniform mesolateral depression; mesotrochantin ca. as long as median width in ventral aspect; metasternum with lateral submarginal groove, median suture complete; tarsomeres and tarsal claws simple simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. Schenkling (1927, as Cosmesus) lists 63 described species, distributed collectively from Venezuela to Chile and Argentina.

RELATIONSHIPS: Possibly the sister group of Ypsilostethus; see Ypsilostethus.

WAY OF LIFE: Nothing appears to be known about the life history or habits of the species in the genus.

MATERIAL EXAMINED: M. electa (Candèze) (1), unidentified species from Venezuela (2).

STATUS: Arnett (1955) pointed out that Schwarz (1906) placed the type species of Cosmesus in Parapomachilius, thus rendering Parapomachilius a junior synonym of Cosmesus. This left the species placed in Cosmesus by Schwarz (1907) and Schenkling (1927) without a name; Arnett (1955) proposed the name Mesembria for these species. The monophyly of Mesembria has not been proven.

14. Genus Dalopius Eschscholtz

Dalopius Eschscholtz, 1829:34. Type species: Elater marginatus Fabricius (designated by Westwood, 1838:25).

DIAGNOSIS: Frontal carina incomplete (Fig. 1G), though only narrowly so in some species; right mandible with conspicuous apicolateral groove, terebral tooth relatively large (Fig. 3D); basistipes of maxilla with only one long seta (Fig. 4E); anterior subpronotal lobe relatively heavily sclerotized with deep notch (Fig. 4I); lateral margin of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron (Figs. 5C, D); margins of mesosternal fossa raised and beaded (Fig. 7D), anterior articulating surface on ventral surface (Figs. 8D, 9D); mesotrochantin ca. as long as median width in ventral aspect (Fig. 8D); metasternum without lateral submarginal groove (Fig. 9D), median suture complete; tarsomeres and tarsal claws simple (Fig. 10A); bursa copulatrix with either dorsal and ventral, various sized, fan-shaped clusters of spines, or discrete spiny plates (Fig. 11H).

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Nearctic and Neotropical Regions. In the Palaearctic region, four described species inhabit Europe and Siberia (Guryeva, 1971) and nine described species are in Japan (Kishii, 1984). Fifty five described species are in Nearctic North America (Brown, 1934; Knull, 1947; Becker, 1956). Blackwelder (1944) records one species from Neotropical West Indies.

RELATIONSHIPS: Sister group to Ancestor M (Fig. 12).

WAY OF LIFE: Natural history data are known for 10 species. The larvae of most recorded species occur in soil, but this may reflect a bias towards agricultural situations. I have reared adults of D. fucatus Brown, D. gentilis Brown, D. mirabilis Brown, D. pallidus Brown and D. suspectus Brown. Larvae of D. fucatus, D. mirabilis and D. pallidus were collected in soil. Soil is recorded as the larval habitat

of D. asellus Brown (Wilkinson, 1963) and D. parvulus Brown (Glen, 1944). Larvae of D. gentilis were collected under moss mats on granitic bedrock and pupae of D. suspectus were collected in leaf litter. Leaf litter is probably the larval habitat of D. tristis Brown (Leech, 1944) and D. vagus Brown (Glen, 1944). The type species of Dalopius has been recorded from soil (Zacharuk, 1963), leaf litter (Leseigneur, 1972; Palm, 1972) and rotten stumps (Platia & Bartolozzi, 1988) in Europe.

Pupation occurs in July and August, and adults overwinter in the pupal cell. The pupal stage lasts about two weeks.

Adults can be collected from May to August, depending on locality, but mainly from late May to mid-July. Adults have been beaten from foliage of trees, collected from flowers and swept from low vegetation. Adults of several unidentified species were attracted to various derivatives of geraniol in pheromone traps in Oregon (Kamm et al., 1983).

A few species are considered serious agricultural pests, though those in leaf litter are considered beneficial as predators of sawfly and lepidopteran pupae.

MATERIAL EXAMINED: OLD WORLD SPECIES: D. ainu Kishii (2), D. exilis Kishii (3), D. marginatus (Linnaeus)* (42), D. miwai Ohira (2), D. patagiatus (Lewis) (2), D. tamui Kishii (4). NEW WORLD SPECIES: D. allegheniensis Knull (2), D. asellus Brown (3), D. cognatus Brown* (19), D. corvinus Brown (5), D. fucatus Brown (8), D. gartrelli Brown (1), D. gentilis Brown (9), D. gracilis Brown (2), D. ignobilis Brown (1), D. improvidus Brown (31), D. insolens Brown (2), D. insulanus Brown (2), D. invidiosus Brown (1), D. jucundus Brown (8), D. maritimus Brown (1), D. mirabilis Brown (23), D. mutabilis Brown (2), D. pallidus Brown (15), D. parvulus Brown (3), D. pennsylvanicus Brown (3), D. plutonicus Brown (3), D. spretus Brown (32), D. suspectus Brown (7), D. tristis Brown (1), D. usitatus Brown (9), D. vagus Brown (43), D. vernus Brown (2), D. vetulus Brown (2), D. virginicus Brown (6), undescribed sp. #5 (35).

STATUS: The Eurasian species have been revised recently (Guryeva, 1971; Kishii, 1984). The North American species require revision. Brown (1934) studied males of the North American species and described 42 new species, but did not apply to his new species any of the species names published prior to his study. Thus, some of Brown's names are undoubtably junior synonyms of older names. Females at present cannot be identified, and I have identified several undescribed species (based on males) from the western

United States.

The North American species may not be monophyletic. Females of the Cognatus group of Brown (1934) lack the fans of spines on the bursa copulatrix characteristic of the type species of Dalopius. Instead, the bursa of the Cognatus group has discrete plates (Fig. 11H) like most species of the Agriotes group.

15. Genus Agriotes Eschscholtz

Agriotes Eschscholtz, 1829:34. Type species: Elater sputator Linnaeus (designated by Westwood, 1838:25).

Ectinus Eschscholtz, 1829: 34. Type species: Elater aterrimus Linnaeus (designated by Westwood, 1838:25). Synonymy by Candèze, 1863:359.

Cataphagus Stephens, 1830:247. Type species: Elater lineatus Linnaeus (by original designation). Synonymy by Candèze, 1863:359.

Pedetes Kirby, 1837:145; preoccupied by Pedetes Illiger (Mammalia). Type species: Elater obscurus Linnaeus (by original designation). Synonymy by Becker, 1956:26.

Agriodrastus Reitter, 1911:222. Type species: Elater pallidulus Illiger (by original designation). Synonymy by Becker, 1956:26.

Tinecus Fleutiaux, 1939:124. Type species: Agriotes (Ectinus) gratiosus Fleutiaux (by original designation). Synonymy by Becker, 1956:26.

Tinecoides Guryeva, 1979b:376. Type species: Agriotes koltzei Reitter (by original designation and monotypy). Described as subgenus of Agriotes.

DIAGNOSIS: Frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral margin of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron (Fig. 5A,B); margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface (subgenus Agriotes) or anterior surface only (subgenus Ectinus); mesotrochantin ca. as long as median width in ventral aspect; metasternum with or without

lateral submarginal groove, median suture complete; tarsomeres and tarsal claws simple; bursa copulatrix either with rounded spiny plates (Fig. 11F), or without spines or spiny plates.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Nearctic, Oriental, Neotropical, Australian, Afrotropical Regions. Schenkling (1927) lists about 160 species from these regions. Thirty-seven species are known from Nearctic North America (Becker, 1956; Knull, 1959); 41 from Neotropical Central America (Schenkling, 1927) and five from Chile (Schenkling, 1927); 76 from the Palearctic region (Guryeva, 1972) plus 12 species assigned to Ectinus (Schenkling, 1927); 38 from Oriental southeast Asia (Schenkling, 1927; Fleutiaux, 1939, 1940a); two from the Afrotropical region (Schenkling, 1927); and one from Australia (Neboiss, 1956).

RELATIONSHIPS: Unresolved (Fig. 12).

WAY OF LIFE: The larvae of most known species live in soil, though this may reflect a bias towards agricultural situations, and the larval habitats for less than 20 species have been recorded. Several species are recorded from leaf litter and humus. Agriotes aterrimus, the type species of the subgenus Ectinus, has been recorded from soil, leaf litter and rotten wood. As a group, larvae of Agriotes occur in a wide range of soil moisture conditions, from humid organic soils to semiarid soils.

Larvae of some species are regarded as obligate phytophages (Kring, 1959), while most seem to be opportunistic feeders on the available live plant and animal food. Larvae are subject to parasitism by mermithid nematodes (Doane et al., 1972).

Data on pupation time is available for six species: five pupate in mid-July and early August, and one (A. pallidulus from Europe) pupates in late May and early June. As is typical for those species which pupate in mid-summer, most adults overwinter in the pupal cell. The pupal stage lasts about two weeks. In the northern hemisphere, adults appear from April to September, but mainly from May to early July. Adults are collected by sweeping low vegetation and by beating trees and shrubs; some are found on flowers and are attracted to fermenting baits.

With such a speciose genus, it is not surprising that adult activity periods are various: some species are recorded as being active only during the day, while others are active at dusk and/or at night. Adults of A. sparsus have been attracted to various derivatives of geraniol in

Oregon (Kamm et al., 1983), and Borg-Karlson et al. (1988) have identified one or two different derivatives of geraniol as the major components of an "uncharacterized abdominal gland" of the female. In the latter study, the geraniol derivatives elicited a strong antennal response in conspecific males.

This genus contains some of the most important agricultural wireworm pests in the world, and species appear to be major pests throughout the range of the genus (Glen, 1944); however, all available data comes from North America and Europe. In those species which are agricultural pests, most damage is done in the second year of a three to five year life cycle.

MATERIAL EXAMINED: Agriotes (sensu stricto): A. babanus Kishii (2), A. brevis Candèze (1), A. elegantulus Lewis (8), A. fulgens Ohira (4), A. gallicus (Boisduval & Lacordaire) (3), A. hirayamai Miwa (2), A. isabellinus (Melsheimer)* (4), A. lineatus (Linnaeus) (2), A. mancus (Say)* (14), A. obscurus (Linnaeus) (1), A. ogurae Lewis (1), A. pallidiangulus Miwa (4), A. pallidulus (Illiger) (3), A. litigiosus (Rossi) (1), A. pilosellus (Schönherr) (2), A. proximus Schwarz (2), A. pubescens Melsheimer (14), A. sparsus LeConte (1), A. sputator (Linnaeus)* (8), A. ustulatus (Schaller) (6). Agriotes (Ectinus): A. apicalis LeConte (15), A. aterrimus (Linnaeus)* (7), A. collaris (LeConte) (2), A. dahuricus persimilis Lewis (2), A. espinosus Becker (1), A. ferrugineipennis (LeConte) (5), A. fucosus (LeConte)* (23), A. insanus Candèze (1), A. limosus (LeConte) (2), A. longicollis Lewis (2), A. mollardi Fleutiaux (6), A. nipponicus Kishii (2), A. oblongicollis (Melsheimer) (16), A. opaculus (LeConte) (7), A. quebecensis Brown (5), A. sericeus Candèze (2), A. somanis Miwa (2), A. stabilis (LeConte) (3), A. tardus Brown (11), A. thevenetii Horn (2), unidentified specimens from Thailand (30, more than 1 species). Agriotes, incertae sedis: A. bivittatus Van Dyke (1), A. criddlei Van Dyke (2).

STATUS: The diagnosis provided above will not separate Agriotes (sensu stricto) from Agriotes (Ectinus), Chatanayus and Insuliectinus. I am not aware of any attempt to apply the putative diagnostic character states of these four taxa to the entire world fauna of Agriotes (sensu lato). The monophyly of Agriotes and Chatanayus remains to be proven.

Of the four species groups recognized by Becker (1956), the Sputator and Sparsus groups belong to Agriotes (sensu stricto) (Guryeva, 1972). Becker (1956) believed the species of his Limosus group could be assigned to

subgenus Ectinus, but preferred to recognize only species groups until the world fauna could be studied. Becker (1956) assigned all of the Mesoamerican species of Agriotes he examined to the Sputator group, all species he examined from eastern Siberia, China and Japan, except A. elegantulus and A. fuscicollis, to the Limosus group and all species from Europe, except A. aterrimus, to the Sputator group. However, with the exception of the above three species, Becker does not specify which species among the "half of the known species" (p. 25) he studied. Guryeva (1972) assigned the Limosus group and an unspecified "large part" (p. 509) of the species from the Indo-Malayan region to Ectinus, which she accords generic status, and transferred Becker's Criddlei group to Dalopius. I believe the latter action is premature. Guryeva cites "the combination of larval and adult characters" (p. 509) as justification for her action. Becker (1956) considered the configuration of the frontal carina and the fan-like clusters of spines on the bursa copulatrix to be diagnostic of the Criddlei group, but acknowledged that the latter character state also is present in Agriotella and Dalopius. Although he included Agriotella in the subtribe Agriotina, he was unable to examine larvae of this genus. The configuration of the frontal carina of the Criddlei group is similar to that of Agriotella. The fan-like clusters of spines on the bursa copulatrix are present in 12 genera of Elaterini and are ancestral for Agriotes (Fig. 12, character 20). Larvae I have examined of Dalopius and Agriotella associated with reared adults cannot be distinguished at present, and I have not examined larvae of the Criddlei group. In the interests of nomenclatural stability, I chose to leave the Criddlei group in Agriotes until its systematic position can be resolved.

In this analysis, Agriotes (sensu stricto) and Agriotes (Ectinus) differed in four character states, but consistently appeared as the sister group of each other. In the type species of Agriotes (sensu stricto), the epipharyngeal bar sclerites are relatively long (as in Fig. 2F), the procoxal cavities are closed dorsally by the proendosternite (Fig. 7B), the anterior articulating surface is on the ventral surface, and the stout setae on the apex of the hind angles of the pronotum are relatively short. In the type species of Agriotes (Ectinus), the epipharyngeal bar sclerites are relatively short (Fig. 2D), the procoxal cavities are open dorsally (as in Fig. 7A), the anterior articulating surface is restricted to the anterior surface, and the stout setae on the apex of the hind angles of the pronotum are relatively long.

The status of Tinecoides is unknown; I have not seen

specimens of the type species.

16. Genus Agriotella Brown

Agriotella Brown, 1933:179. Type species: Elater bigeminatus Randall (by original designation).

DIAGNOSIS: Frontal carina complete, curved towards the anterior margin of the frons; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin ca. as long as median width in ventral aspect; metasternum without lateral submarginal groove, median suture complete; tarsomeres and tarsal claws simple; bursa copulatrix with dorsal and ventral fan-shaped clusters of spines; northern hemisphere.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic and Palaearctic Regions. Of the nine described species in this genus, four live in Palaearctic southern Europe (placed by most authors in Idolus Desbrochers) (Schenkling, 1925) and five in Nearctic North America, ranging collectively across Canada and south in the western mountains to California and Colorado, and in the Appalachians to Georgia (Brown, 1933; Lane, 1965).

RELATIONSHIPS: Unresolved (Fig. 12).

WAY OF LIFE: Little is known about the life history or habits of Agriotella. I have reared A. bigeminata (Randall) and A. occidentalis Brown from larvae collected in humus-rich soil under moss on bedrock, and have collected adults of A. occidentalis under rocks and by beating branches of Picea. In France and Italy, adults of A. picipennis (Bach) have been collected by beating various trees and shrubs, and are also found on various herbs and grasses; adults are active from May to August (Leseigneur, 1972, as Idolus; Platia & Bartolozzi, 1988). Thomas (1941) reports adults of A. bigeminata in Pennsylvania are common on spruce in June.

MATERIAL EXAMINED: A. bigeminata (Randall) (12), A. occidentalis Brown (13), A. californicus (Schaeffer) (2), A. columbiana Brown (1), A. picipennis (Bach) (33).

STATUS: This genus has not been revised in its entirety and has not been shown to be monophyletic. I have found no

character states which will distinguish it from Cosmesus (q.v.)

17. Genus Cosmesus Eschscholtz

Cosmesus Eschscholtz, 1829:33. Type species: Cosmesus bilineatus Eschscholtz (by monotypy).

Parapomachilius Schwarz, 1900b:339. Type species: Parapomachilius incertus Schwarz (designated by Hyslop, 1921:662). Synonymy by Arnett, 1955:601.

DIAGNOSIS: As in Agriotella, except: South America.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The 10 described species in this genus live in Brazil and Paraguay (Schenkling, 1925, as Parapomachilius).

RELATIONSHIPS: Unresolved (Fig. 12).

WAY OF LIFE: Nothing appears to be known about the life history or habits of the species in the genus.

MATERIAL EXAMINED: C. sp. near bilineatus Eschscholtz (5), unidentified species from Paraguay (14).

STATUS: The distinction between Cosmesus and Agriotella appears to be subtle at best. Other than geography, I have not found any characters that will separate these two genera. I have not seen the type material of C. bilineatus. I have examined four specimens identified as C. bilineatus from the United States National Museum and one from the Canadian National Collection of Insects. These two series differ from each other in character states of the female genitalia and colour pattern. I do not believe the two series are conspecific with each other, but I do not know which is C. bilineatus.

18. Genus Deromecus Solier

Deromecus Solier, 1851:11. Type species: Deromecus angustatus Solier (designated by Hyslop, 1921:639).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons (Fig. 1D); right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised

and beaded, anterior articulating surface on ventral surface; mesotrochantin ca. as long as median width in ventral aspect; metasternum with lateral submarginal groove (Fig. 9E), median suture complete; tarsomeres and tarsal claws simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The genus contains at least 34 described species (Schenkling, 1925) collectively ranging from Mexico to southern Chile. Almost all species were described from Chile.

RELATIONSHIPS: Unresolved (Fig. 12).

WAY OF LIFE: Nothing is known about the life history or habits of the species in this genus.

MATERIAL EXAMINED: D. attenuatus Solier (1), D. filicornis Solier (1), D. impressus (Solier) (2), D. vulgaris Solier* (16), unidentified species from Chile (4).

STATUS: The monophyly of this genus has not been proven.

19. Genus Medonia Candèze

Medonia Candèze, 1860:3. Type species: Bedresia punctato-sulcata [sic] Solier (by monotypy).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; right mandible with conspicuous apicolateral groove; basistipes of maxilla with only one long seta; lateral carina of pronotum divided by hind angles, carina meeting anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum without lateral submarginal groove, median suture complete; tarsomere 4 lobed, tarsal claws simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The genus contains four described species, all of which live in Chile (Schenkling, 1925).

RELATIONSHIPS: Sister group of Pseudoderomecus (Fig. 12).

WAY OF LIFE: Label data on a specimen of M. punctatosulcata state the specimen was collected in a Nothofagus - Podocarpus association. Nothing else seems to be known about the life history or habits of these species.

MATERIAL EXAMINED: M. punctatosulcata (Solier) (7)

STATUS: The genus has not been revised in its entirety. The divided lateral carina of the pronotum is an autapomorphy of Medonia.

20. Genus Pseudoderomecus Fleutiaux

Pseudoderomecus Fleutiaux, 1907:186. Type species: Medonia fairmairei Candèze (by monotypy).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum distinctly dorsad mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on anterior surface only; lateral lobes of mesosternum with subreniform mesolateral depression; mesotrochantin ca. twice as long as median width in ventral aspect; metasternum without lateral submarginal groove, median suture complete; tarsomere 4 lobed, tarsal claws simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The genus contains one described species and at least one undescribed species, both of which live in Chile.

RELATIONSHIPS: Sister group of Medonia (Fig. 12).

WAY OF LIFE: Nothing is known about the life history or habits of this genus.

MATERIAL EXAMINED: P. fairmairei (Candèze), type series (1 male, 2 females), undescribed species from Chile* (11).

STATUS: The genus has not been revised and its monophyly is unproven.

21. Genus Betarmon Kiesenwetter

Betarmon Kiesenwetter, 1858:265. Type species: Elater bisbimaculatus Schönherr (designated by Hyslop, 1921:631).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long

seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin ca. as long as median width in ventral aspect; metasternum without lateral submarginal groove, median suture complete; tarsomere 3 lobed, tarsal claws simple; bursa copulatrix with dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The type species is the only species included in this genus; it lives in north and central Europe (Schenkling, 1925).

RELATIONSHIPS: Sister group of (Pomachilius + Paracosmesus) (Fig. 12).

WAY OF LIFE: The larva is apparently a soil-dweller, occurring under large stones in slightly humid areas; in France, adults are active mainly in June and July in sunny places around bodies of water. They are collected by beating willows and poplar, and are active mainly at dusk (Leseigneur, 1972). In Italy, adults are found under plant debris by rivers and streams from mountain headwaters to lowland river mouths; adults are attracted to lights (Platia & Bartolozzi, 1988).

MATERIAL EXAMINED: B. bisbimaculatus (Schönherr)* (6).

STATUS: The distinction between Betarmon and Pomachilius may not survive a revision of the species of Pomachilius. The size of the raised margins of the mesosternal fossa, considered diagnostic by Schwarz (1906), is not necessarily diagnostic. The margins of the mesosternal fossa are only slightly more prominent in Pomachilius suturalis Candèze than in Betarmon. In the specimens of Pomachilius I have examined, the mesotrochantin is concealed in ventral aspect, while the mesotrochantin is visible in Betarmon; more study is required.

22. Genus Paracosmesus Schwarz

Paracosmesus Schwarz, 1901:38, new name for Pomachilioides Schwarz, 1900b:344, preoccupied by Pomachilioides Candèze, 1897:51. Type species: Pomachilioides cruciatus Schwarz (designated by Hyslop, 1921:666).

DIAGNOSIS: Frontal carina incomplete or complete and curved to join anterior margin of frons (Fig. 1F); right mandible

with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum without lateral submarginal groove, median suture complete; tarsomere 3 lobed, tarsal claws simple; bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. Schenkling (1927) lists 7 described species from Peru and Bolivia. I assign specimens from Paraguay to this genus.

RELATIONSHIPS: Sister group of Pomachilius (Fig. 12).

WAY OF LIFE: Nothing seems to be known about the life history or habits of the species of Paracosmesus.

MATERIAL EXAMINED: P. cruciatus (Schwarz), type series (7 specimens, males and females), two or three unidentified species from Paraguay* (59).

STATUS: Character states visible externally and those of the female genitalia are taken from the type series of Paracosmesus cruciatus (Schwarz) from the Deutsches Entomologisches Institut, Eberswalde-Finow. Internal character states and those not visible in the type series are taken from an unidentified species from Paraguay, which differs somewhat from P. cruciatus. In P. cruciatus, the lobe on tarsomere 3 is quite distinct, but in the species from Paraguay, the lobe is much smaller and rather indistinct. I am reasonably confident the two species are congeneric, but the difference in size of the lobes on the tarsomeres suggests this character is not reliable as a diagnostic character of Paracosmesus.

23. Genus Pomachilius Eschscholtz

Pomachilius Eschscholtz, 1829:31. Type species: Elater subfasciatus Germar (by monotypy).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; distal angles of antennomeres not produced; anterior subpronotal lobe relatively heavily sclerotized with deep

notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum with or without lateral submarginal groove, median suture complete; tarsomere 3 lobed (Fig. 10B), tarsal claws simple (Fig. 10E); bursa copulatrix with large dorsal and ventral fan-shaped clusters of spines.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. There are about 100 described species in Pomachilius (Schenkling, 1925) ranging collectively from Costa Rica to northern Argentina and northern Chile.

RELATIONSHIPS: Sister group of Paracosmesus (Fig. 12).

WAY OF LIFE: Little is known about the life history or habits of the species in this genus. I have collected adults of P. spinifer Champion from trailside vegetation in cloud forest in Costa Rica. I have seen a reared specimen of Pomachilius in the Smithsonian Institution, Washington, DC, collected at São Paulo, Brazil and identified as Pomachilius brunneus? Candèze; the larval head capsule is covered with sand grains and label data indicate larval habitat as soil.

MATERIAL EXAMINED: P. spinifer Champion (5), P. aeloides Candèze (1), P. centrurus Candèze (1), P. suturalis Candèze (2), P. cuspidatus Candèze (2), P. hiosurus Candèze (1), P. linearis Candèze* (6), P. brunneus ? Candèze (1), P. sp. near mucronatus Champion (1), four unidentified species (1 each).

STATUS: The monophyly of this genus is unproven. The diagnostic characters of Pomachilius, Smilicerus, Paracosmesus, Betarmon and Agriotella/Cosmesus require critical reappraisal. I am not convinced that the character states used diagnose discrete taxa.

24. Genus Adrastus Eschscholtz

Adrastus Eschscholtz, 1829:35. Type species: Elater limbatus Fabricius (by monotypy).

DIAGNOSIS: Periocular pits absent (Fig. 1H); frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; mesosternal fossa

with margins raised and beaded (Fig. 7G), anterior articulating surface on ventral surface; mesotrochantin ca. as long as median width in ventral aspect; metasternum with lateral submarginal groove, median suture complete; tarsomeres simple, tarsal claws pectinate; bursa copulatrix without spines or spiny plates.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The 14 described species of Adrastus (Guryeva, 1976, 1979a; Platia & Schimmel, 1991b), range collectively from Europe and North Africa in the west to Siberia in the east.

RELATIONSHIPS: Sister group of all other taxa in the Adrastus group (Fig. 12).

WAY OF LIFE: Adults of the European species have been collected mainly by beating shrubs and sweeping low vegetation (Leseigneur, 1972; Rudolph, 1982; Platia & Bartolozzi, 1988). Lowland species appear as adults mainly in June and July, while more montane species appear as adults mainly in July and August (Leseigneur, 1972). In France, adults of A. limbatus (Fabricius) are mainly diurnal, those of A. axillaris Erichson are mainly crepuscular, and those of A. pallens (Fabricius) are mainly nocturnal; many species seem to prefer cool, moist areas (Leseigneur, 1972). Larvae are apparently soil dwellers, preferring meadows and upland meadows, though some are found in forests (Guryeva, 1976). A larva of A. nitidulus Marsh was collected in a bumble bee nest and reared to adult, and another of either this species or A. pallens was collected in leaf litter (Palm, 1972).

MATERIAL EXAMINED: A. pallens (Fabricius)* (3), A. limbatus (Fabricius) (2), A. rachifer (Geoffroy) (13), A. binaghii Leseigneur (8), A. lacertosus Erichson (2), A. axillaris Erichson (2), A. kryshtali Dolin (2).

STATUS: Guryeva (1976) published a key to species of Adrastus, but the monophyly of the genus has not been demonstrated to the best of my knowledge.

25. Genus Synaptus Eschscholtz

Synaptus Eschscholtz, 1829:32. Type species: Elater filiformis Fabricius (designated by Hyslop, 1921:671).

DIAGNOSIS: Periocular pits relatively deep, subcircular (Fig. 1I); frontal carina incomplete; right mandible with conspicuous apicolateral groove (Figs, 3F, G), terebral tooth relatively large (Fig. 3J); basistipes of maxilla

with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; prosternal mucro with ventral surface narrower than dorsal surface, subapical tooth unidentate; mesosternum with fossal margins raised and beaded, anterior articulating surface on ventral surface; mesotrochantin ca. as long as median width in ventral aspect; metasternum with lateral submarginal groove, median suture complete; tarsomere 3 lobed, tarsal claws pectinate (Fig. 10G); bursa copulatrix with spiny plates, posterior end of plates conspicuously attenuated.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic, Oriental Regions. There are two described species, one living in Europe, Siberia and the Middle East (Schenkling, 1927) and the other in Vietnam (Fleutiaux, 1940c).

RELATIONSHIPS: Sister group of Parasilesis + a polychotomy of Ctenoplus, Peripontius, Glyphonyx and Silesis (Fig. 12).

WAY OF LIFE: The larva is apparently unknown; adults live in cool, humid areas such as marshes, around bodies of water, and forests, and may be collected by beating shrubs and trees, and sweeping herbs and grasses. In France, adults are active from May to August at elevations below 1000m (Leseigneur, 1972).

MATERIAL EXAMINED: S. filiformis (Fabricius)* (13).

STATUS: The genus has not been revised, and its monophyly is unproven.

26. Genus Parasilesis Ohira

Parasilesis Ohira, 1990:75. Type species: Silesis musculus Candèze (by original designation).

DIAGNOSIS: Periocular pits relatively deep, subcircular; frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; prosternal mucro with tridentate subapical tooth (Fig. 6F); margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum with lateral submarginal groove, median suture reduced anteriorly (Fig. 9B); tarsomere 4 lobed, tarsal claws pectinate; bursa copulatrix with spiny plates, posterior end of plates

conspicuously attenuated.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The genus is monobasic. P. musculus lives in Japan.

RELATIONSHIPS: Sister group to a polychotomy involving Ctenoplus, Glyphonyx, Peripontius and Silesis (Fig. 12).

WAY OF LIFE: Unknown.

MATERIAL EXAMINED: P. musculus Candèze* (3).

STATUS: Ohira (1990) hypothesized that Silesis and Parasilesis are closely related. However, Parasilesis was proposed without examining all species of Silesis, so the diagnostic character states presented above and by Ohira (1990) may be autapomorphies for P. musculus. The diagnostic character states of Parasilesis, Silesis and Peripontius require critical study.

27. Genus Ctenoplus Candèze

Ctenoplus Candèze, 1863:463. Type species: Ctenoplus javanensis Candèze (by monotypy).

DIAGNOSIS: Periocular pits relatively shallow, irregular in shape (Fig. 1J); frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded anteriorly, raised and thickened between mesocoxae (Fig. 7F), anterior articulating surface on ventral surface; lateral lobes of mesosternum with subreniform mesolateral depression (Fig. 7F); mesotrochantin concealed in ventral aspect; metasternum with lateral submarginal groove, without median suture; tarsomeres without lobes, tarsal claws pectinate; bursa copulatrix with spiny plates and patches of spines, posterior end of plates conspicuously attenuated.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Oriental Region. The eight described species of Ctenoplus are distributed collectively from Thailand and Vietnam to Borneo and Java. I have seen an undescribed species from eastern India.

RELATIONSHIPS: Unresolved. Ctenoplus forms a polychotomy with Peripontius, Glyphonyx and Silesis (Fig. 12; see also

Figs. 18, 19).

WAY OF LIFE: Little is known about the life history or habits of these species. I collected two specimens of C. brunneus Fleutiaux in northern Thailand at 1300m elevation; one was attracted to ultraviolet light, the other was collected from vegetation within a predominately pine forest at the same site. A specimen of Ctenoplus nitidipennis Schwarz from Brunei was captured in a malaise trap.

MATERIAL EXAMINED: C. javanensis Candèze, (holotype female), C. nitidipennis Schwarz, (1 syntype, 27 non-types), C. nigripennis Schwarz, (2 syntypes), C. collaris Candèze, (3 syntypes), C. sanguinolentus (Candèze), (4 syntypes), C. brunneus Fleutiaux* (2), an undescribed species from each of Java (1), Sumatra (4), and India (7).

STATUS: Ctenoplus has not been revised and its monophyly is unproven. I am revising the genus.

28. Genus Peripontius Guryeva

Peripontius Guryeva, 1979b:314; new name for Cratonychus Reiche & Saulcy, 1857:410, preoccupied by Cratonychus Dejean, 1833. Type species: Cratonychus dimidiatus Reiche & Saulcy (by monotypy).

DIAGNOSIS: Periocular pits relatively deep, subcircular; frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; ventral surface of prosternal mucro narrower than dorsal surface, subapical tooth unidentate (Fig. 6H); mesosternal fossa with margins raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum with lateral submarginal groove, without median suture; tarsomere 4 lobed, tarsal claws pectinate; bursa copulatrix with spiny plates, posterior end of plates conspicuously attenuated.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The four species included in this genus by Guryeva (1979b) live in southern Europe and North Africa. Platia & Schimmel (1991b) included three additional species.

RELATIONSHIPS: Unresolved. See Ctenoplus.

WAY OF LIFE: In France and Italy, adults of P. terminalis (Erichson) occur in May and June, and are collected by beating oaks and willows, and sweeping vegetation along river banks. They have also been found under bark in winter (Leseigneur, 1972, as Silesis; Platia & Bartolozzi, 1988).

MATERIAL EXAMINED: P. terminalis (Erichson)* (8).

STATUS: Guryeva (1979b) compared Peripontius with Silesis and included in it species previously placed in Silesis. According to the figures cited by Guryeva (1979b), Peripontius is distinguished from Silesis by the shape of the prosternal mucro and the shape of the metacoxal plate. In Peripontius, the ventral surface of the prosternal mucro is narrower than the dorsal surface and the metacoxal plate is much wider mesally than laterally. In Silesis, the ventral surface of the prosternal mucro is wider than the dorsal surface and the metacoxal plate is subparallel for its entire width.

I have seen only one species of Peripontius, and only a few species of Silesis. In those species, the metacoxal character cited above appears to be too variable to be reliable. The genus has not been demonstrated to be monophyletic and the number of included species must await examination of the species of Silesis from southeast Asia.

29. Genus Glyphonyx Candèze

Glyphonyx Candèze, 1863:451. Type species: Glyphonyx gundlachii Candèze (designated by Hylsop, 1921:647).

Microglyphonyx Champion, 1896:549. Type species: Microglyphonyx coarctatus Champion (by monotypy). Synonymy by Schwarz, 1907:291, 293

DIAGNOSIS: Periocular pits relatively deep, subcircular (Fig. 1E); frontal carina complete (Fig. 1E) or not, if incomplete, supraantennal crests separated along anterior margin of frons by less than one-quarter length of labrum; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect (Fig. 8A); metasternum with lateral submarginal groove, without median suture (Fig. 9C); tarsomere 4 (Fig. 10C) or

tarsomeres 3 and 4 (Fig. 10D) lobed, tarsal claws pectinate; bursa copulatrix with spiny plates, posterior end of plates conspicuously attenuated (Fig. 11G). See Status below.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Nearctic, Neotropical, Afrotropical, Oriental and Palaearctic Regions. Sixteen described species inhabit Nearctic North America (Smith & Balsbaugh, 1984), distributed collectively from Ontario to Florida and west to Arizona. Schenkling (1927) lists 30 species from Neotropical Central America and four from Colombia and Peru. The genus is represented in the Afrotropical region by only three described species which live in west-central Africa and Reunion (Schenkling, 1927), but is quite speciose in Oriental southeast Asia with 62 described species collectively ranging from eastern India to the Philippine archipelago and Java (Schenkling, 1927, Fleutiaux, 1940c). One described species inhabits Palaearctic Japan.

RELATIONSHIPS: Unresolved. See Ctenoplus.

WAY OF LIFE: Little is known about the life history or habits of species of Glyphonyx. Larvae of G. bimarginatus Schaeffer and G. recticollis (Say) occur in soil (Smith & Balsbaugh, 1984; Cheshire & Jones, 1988). One generation per year is recorded for a population of G. recticollis in the southern United States, but an unidentified species from Mexico has two generations per year (Smith & Balsbaugh, 1984). Adults are attracted to fermenting baits (Frost & Dietrich, 1929) and lights. Specimens I collected in Thailand were obtained from: malaise traps; picked from roadside vegetation; and at ultraviolet lights.

G. recticollis is considered to be a pest by Cheshire & Jones (1988).

MATERIAL EXAMINED: G. inquinatus (Say)* (1), G. testaceus (Melsheimer) (2), G. sp. near championi Smith & Balsbaugh* (1), G. dalopioides (1), G. liukuiensis (1), unidentified specimens from United States (78, more than 1 species), Costa Rica (12, more than 1 species), Ecuador (2) and Thailand* (51, more than 1 species).

STATUS: I have not seen specimens of the type species of either Glyphonyx or Microglyphonyx and the status of Microglyphonyx is unresolved. As elaterid genera are traditionally defined, New and Old World species of Glyphonyx would be placed in different genera. New World species have tarsomere 4 lobed (Smith & Balsbaugh, 1984), while Old World species have tarsomeres 3 and 4 lobed (Fleutiaux, 1940c). New and Old World species also differ

in the position of the dorsal periocular pit. In the Old World species I have examined, the dorsal periocular pit is contiguous with the supraantennal crest, while in the New World species, it is distinctly ventrad the supraantennal crest. A revision of the genus is required to determine whether these differences warrant recognizing two genera.

30. Genus Silesis Candèze

Silesis Candèze, 1863:458. Type species: Silesis hilaris Candèze (designated by Hyslop, 1921:669).

Okinawana Kishii, 1976:54. Type species: Silesis hatayamai Kishii (by monotypy and original designation). Synonymy by Ohira, 1990:74-75.

DIAGNOSIS: Periocular pits relatively deep, subcircular; frontal carina incomplete; right mandible with conspicuous apicolateral groove, terebral tooth relatively large; basistipes of maxilla with only one long seta; anterior subpronotal lobe relatively heavily sclerotized with deep notch; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; ventral surface of prosternal mucro as wide as dorsal surface, subapical tooth unidentate (Fig. 6G); margins of mesosternal fossa raised and beaded, anterior articulating surface on ventral surface; mesotrochantin concealed in ventral aspect; metasternum with lateral submarginal groove, without median suture; tarsomere 4 lobed, tarsal claws pectinate; bursa copulatrix with linear spiny plates, posterior end of plates conspicuously attenuated.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic and Oriental Regions. Schenkling (1927) and Fleutiaux (1940a, c) list 46 described species ranging collectively from the Palaearctic Mediterranean region east to Japan and south to Oriental India, and Borneo and Sumatra in the Indo-Australian archipelago. Platia & Schimmel (1991a, 1993b) described 56 new species, mainly from Nepal and northern India.

RELATIONSHIPS: Unresolved. See Ctenoplus.

WAY OF LIFE: In France, adults of S. rutilipennis (Illiger) occur in May and June, and are found under marsh debris and under rocks by bodies of water; they can also be collected by beating willows and poplar, and have been found in winter under flood debris and under peeling bark (Leseigneur, 1972).

MATERIAL EXAMINED: S. grisescens Candèze* (3), unidentified species from Thailand (3) and Nepal (5).

STATUS: This genus has not been shown to be monophyletic. Both Peripontius and Parasilesis were proposed for species previously assigned to Silesis, but Silesis was not revised at the same time to make sure the diagnostic characters proposed for the former two genera were reliable.

Elaterini incertae sedis

31. Genus Chatanayus Fleutiaux

Chatanayus Fleutiaux, 1939:124. Type species: Agonischius ruficollis Fleutiaux, 1903, nec Schwarz, 1900a (=Agonischius Fleutiauxi Schwarz) (by monotypy).

Neoagriotes Ohira, 1962b:263. Type species: Agriotes insularis Miwa (by monotypy and original designation). Synonymy by Ohira, 1973b:99, 101

DIAGNOSIS: Frontal carina incomplete; basistipes of maxilla with only one long seta; lateral carina of pronotum joining anterior margin of pronotom at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded; tarsomeres and tarsal claws simple; lateral lobes of male genitalia relatively wide, straight and truncate apically (Fleutiaux, 1939). See Status below.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Oriental and Palaearctic Regions. Fleutiaux (1939) proposed this genus for the type species from Oriental Vietnam. Kishii (1987) includes two Japanese species.

RELATIONSHIPS: Unknown.

WAY OF LIFE: Unknown.

MATERIAL EXAMINED: C. ishiharai Nakane & Kishii (1 male).

STATUS: Chatanayus is assigned to the Elaterini based on examination of a male of C. ishiharai kindly loaned to me by by Dr. T. Kishii. The male genitalia appears to be distinctive, but the degree of development of the carina on the hind angles of the pronotum is open to interpretation. Both of these character states were used by Fleutiaux (1939) to diagnose Chatanayus. All of the characters used to define this genus need to be reappraised relative to Agriotes. Additional specimens of Chatanayus need to be examined before the status and systematic position of this taxon can be determined.

32. Genus Insuliectinus Kishii

Insuliectinus Kishii, 1984:12-13. Type species: Insuliectinus amami Kishii (by original designation and monotypy).

DIAGNOSIS: Frontal carina incomplete; basistipes of maxilla with only one long seta; margins of mesosternal fossa raised and beaded; fourth antennomere longer than the second and third antennomeres combined (Kishii, 1984, 1987), lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; hind angles of the pronotum without a carina (Kishii, 1984, 1987); anterolateral projection of the prosternum acute (Kishii, 1984); tarsomeres and tarsal claws simple.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The genus is monobasic and lives in Japan.

RELATIONSHIPS: Unknown.

WAY OF LIFE: Unknown.
MATERIAL EXAMINED: I. amami Kishii, holotype.

STATUS: The holotype male is the only known specimen representing this genus. I have examined this specimen through the kindness of Dr. T. Kishii. More specimens are required before the status of this genus can be determined. The anterolateral projection of the prosternum is the largest one I have seen in Elaterini.

33. Genus Panspoeus Sharp

Panspoeus Sharp, 1877:409. Type species: Panspoeus guttatus Sharp (by monotypy).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; hypomeron grooved ventrad lateral carina of pronotum; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa not raised and beaded; tarsomeres and tarsal claws simple.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Australian Region. The genus contains only one species (Owen et al., 1985). It was described from New Zealand and has been introduced into England.

RELATIONSHIPS: Unknown. The systematic position of the genus is somewhat enigmatic. The configuration of the gena places it within the Elaterini. The margins of the mesosternal fossa are neither raised nor beaded (Owen et

al., 1985, fig. 3), a character state that associates Panspoeus with the Elater group. However, unlike other taxa of the Elater group (with the possible exception of Leptoschema), the bursa copulatrix bears discrete plates. Further comments are deferred until additional specimens can be studied.

WAY OF LIFE: The life history and habits of Panspoeus are not well known. In New Zealand, P. guttatus is widespread in forested areas on both North and South Islands and has been beaten from Nothofagus. In England, specimens have been collected by beating herbage and sweeping reeds; they are also described as being more active than other elaterids (Owen et al., 1985). Parthenogenesis is suspected in the English (and possibly New Zealand) populations since all known specimens from England are females (Owen et al., 1985).

MATERIAL EXAMINED: P. guttatus Sharp, type series (2 females).

STATUS: The genus was revised by Owen et al. (1985), who chose not to assign it to any family-group category. I have seen only two specimens, the type series of P. guttatus from the Natural History Museum, London. The modification of the hypomeron is an autapomorphy of Panspoeus. The hypomeron bears a rounded groove, presumably for the reception of the antennae, immediately ventrad and parallel with the lateral carina of the pronotum (Owen et al., 1985, fig. 2).

Panspoeus is the only representative of the Elaterini known to me from the Australian region. If P. guttatus is parthenogenetic, the possibility that Panspoeus was introduced into New Zealand should be considered. Males of P. guttatus have been collected in New Zealand, but this is not necessarily evidence against parthenogenesis in this species. Both parthenogenetic and bisexual populations of Hypnoidus bicolor (Eschscholtz) inhabit the Prairie provinces of Canada. Parthenogenetic populations of H. bicolor predominate in the northern parts of these provinces and bisexual populations predominate in parts of the south, with a zone of integradation between them (Zacharuk, 1958b, as Hypolithus Eschscholtz). One can speculate that if Panspoeus was introduced into New Zealand, the source of the specimens could have been from a population containing both bisexual and parthenogenetic forms.

34. Genus Pseudagriotes Schwarz

Pseudagriotes Schwarz, 1896:103. Type species:

Pseudagriotes holtzi Schwarz (by monotypy).

DIAGNOSIS: Frontal carina incomplete; margins of mesosternal fossa not raised and beaded; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; prosternal mucro gently sloping dorsally; mesepimeron with anterolateral projection; metacoxal plate only slightly enlarged at level of trochanter-femur joint; tarsomere 4 with small, short lobe, tarsal claws simple.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Palaearctic Region. The genus contains only one species, described from Turkey.

RELATIONSHIPS: Unknown. Since the margins of the mesosternal fossa are neither raised nor beaded, Pseudagriotes, like Panspoeus, is more closely related to taxa of the Elater group than to those of the Pomachilius, Agriotes and Adrastus groups.

WAY OF LIFE: Unknown.

MATERIAL EXAMINED: P. holtzi Schwarz, type series (2 males).

STATUS: The specimens of the type series are the only ones of this genus I have examined. The status and systematic position of Pseudagriotes remain unresolved until more data can be collected.

35. Genus Smilicerus Candèze

Smilicerus Candèze, 1860:20. Type species: Smilicerus sallei Candèze (designated by Hyslop, 1921:670).

DIAGNOSIS: Frontal carina complete, horizontal, distinctly separated from anterior margin of frons; antennomeres relatively wide, anterodistal and posterodistal angles produced; right mandible with conspicuous apicolateral groove; basistipes of maxilla with only one long seta; lateral carina of pronotum joining anterior margin of pronotum at same point as mesal margin of hypomeron; margins of mesosternal fossa raised and beaded; metasternum without lateral submarginal groove; tarsomere 3 lobed, tarsal claws simple.

GEOGRAPHICAL DISTRIBUTION AND INCLUDED TAXA: Neotropical Region. The genus contains five described species distributed collectively from Nicaragua to Bolivia (Blackwelder, 1944).

RELATIONSHIPS: Unknown, though probably very closely related to Pomachilius.

WAY OF LIFE: Unknown.

MATERIAL EXAMINED: S. sallei Candèze (2), S. zonatus Candèze (1), unidentified species from Costa Rica (1) and Ecuador (1).

STATUS: This genus has never been revised and has not been shown to be monophyletic.

GENERA EXCLUDED FROM ELATERINI

The following genera have been included in the traditional definitions of the Elaterini, Pomachiliini, Agriotini and Adrastini. All of them lack the genal apomorphy that would include them in the Elaterini as I have defined it. With the exception of the Sericosomini, the placements suggested below must be considered tentative. My knowledge of taxa outside of the Elaterini is quite limited, and the placements suggested below are designed to associate the names with possible relatives for further investigation. Possible placements of taxa excluding Sericosomini are summarized in Table 1.

Elaterinae: Sericosomini

The Sericosomini are the outgroup to the Elaterini (Fig. 12). They share with the Elaterini the derived character state, ventral margin of gena diverging anteriorly from ventral margin of eye (Fig. 1B). However, I have not found an autapomorphy for the Sericosomini and difficulties polarizing character states of the ingroup indicate the Sericosomini are not a monophyletic group. Like almost all elaterid taxa, this tribe requires revision.

The number of genera included in Sericosomini is uncertain at present. I am tentatively placing Dolerosomus in the Sericosomini until the definition and relationships of the tribe can be determined. A family-group name based on Dolerosomus was proposed by Dolin (1975), but the name is a nomen nudum. I am placing Sericus Eschscholtz, Agonischius Candèze, Chiagosnius Fleutiaux, Sadoganus Ohira, and tentatively, Ectinoides Kishii and Vuilletus Fleutiaux in Sericosomini. The placement of Dolerosomus, Ectinoides and Vuilletus in Sericosomini is tentative since these three genera differ from Sericus, Agonischius, Sadoganus and Chiagosnius in the form of the gena. The anterior margin of the gena in Dolerosomus differs in being quite narrow and carinate marginally and submarginally; in Sericus, Agonischius, Sadoganus and Chiagosnius, the anterior margin of the gena is much wider dorsally and is carinate submarginally ventrad the mandible. In Ectinoides and Vuilletus, the gena does not have a distinct subapical carina by the ventral condyle of the mandible.

Specimens of Sericus incongruus (LeConte), Dolerosomus silaceus (Say) and Chiagosnius obscuripes (Gyllenhal) were used to determine the character states of the outgroup, since these are the only members of the outgroup for which specimens were available for detailed study. Sericus incongruus is either conspecific with or closely related to

the type species of Sericus, S. brunneus (Linnaeus). Dolerosomus silaceous is either conspecific with (Roache, 1961) or closely related to (Lane, 1971) the type species of Dolerosomus, D. debilis (LeConte). Chiagosnius obscuripes is the type species of that genus.

Nomenclaturally, in the use of Sericosomini, I am disagreeing with the interpretation of Stibick (1979), who considered both Sericosomini and "Dolerosomini" unacceptable. Stibick, following Roache (1961), considered Dolerosomus a junior subjective synonym of Sericus; he apparently overlooked the work of Lane (1971), who resurrected Dolerosomus from synonymy with Sericus. "Dolerosomini" would be a valid name for a tribal group that includes Dolerosomus, except "Dolerosomini Dolin, 1975" is a nomen nudum. Sericosomini is based on Sericosomus Dejean, an isogenotypic synonym of Sericus. Stibick believed that Recommendation 40A of the Code of Zoological Nomenclature required a new name based on Sericus be proposed for Sericosomini; Recommendation 40A deals with citation of author and date, not replacement of names. Under Article 40 of the Code (International Trust for Zoological Nomenclature, 1985), it is clear to me that a replacement name for Sericosomini is unnecessary and I continue to use this name.

Sericus Eschscholtz, 1829:34. Type species: Elater brunneus Linnaeus (designated by Hyslop 1921:669).

Sericosomus Dejean 1833:39. Type species: Elater brunneus Linnaeus (designated by Westwood, 1838:25). Isogenotypic with Sericus.

Schenkling (1927) lists 15 species in this genus; these live collectively in Eurasia and North America. As defined by Roache (1961), Sericus is not monophyletic. Lane (1971) restricts the name to those species congeneric with S. brunneus and resurrects Dolerosomus Motschulsky for most of the remaining North American species. Elater honestus Randall, the senior synonym of Atractopterus fusiformis LeConte, Sericus rugosus Van Dyke and Dolopius sericarius Motschulsky are not congeneric with S. brunneus; I have transferred them to Atractopterus.

MATERIAL EXAMINED: S. brunneus (Linnaeus) (5), S. incongruus (LeConte) (25), S. viridanus (Say) (3), S. bifoveolatus (Lewis) (1).

Agonischius Candèze, 1863:407. Type species: Agonsichius pectoralis Candèze (designated by Hyslop, 1921:624).

Vuilletus Fleutiaux, 1939:123. Type species: Agonischius altus Candèze (by original designation).

Chiagosnius Fleutiaux, 1939:136. Type species: Elater obscuripes Gyllenhal (by original designation).

Vuilletus and Chiagosnius are based upon species formerly included in Agonischius. Collectively these three genera contain more than 150 described species, distributed from Japan to India and southeast to Australia, but since a revision of these genera has never been made, the number of species in each genus is unknown to me.

MATERIAL EXAMINED: C. obscuripes (Gyllenhal) (8), V. peropacus (Nakane) (1), V. subopacus (Nakane) (1), V. viridis (Lewis) (1), A. pectoralis Candèze (1), A. thoracicus Fleutiaux (1).

Dolerosomus Motschulsky 1859:382. Type species: Dolerosomus flavipennis Motschulsky (designated by Hyslop 1921:641).

Considered congeneric with Sericus by Candèze (1863:427), this genus was resurrected by Lane (1971) for the Nearctic species, Elater silaceus Say, Sericosomus debilis LeConte (the senior synonym of D. flavipennis Mots.) and Agriotes blaisdelli Van Dyke. Representatives also live in Japan.

MATERIAL EXAMINED: D. debilis (LeConte) (38), D. silaceus (Say) (25), D. blaisdelli (Van Dyke) (14), D. gracilis (Candèze) (4).

Ectinoides Kishii, 1966: 40. Type species: Agriotes leucophaeatus Kishii (=Megapenthes insignitus Lewis) (by monotypy and original designation).

Ectinoides is a monobasic genus living in Japan (Kishii, 1987). Agriotes leucophaeatus Kishii is preoccupied by A. leucophaeatus Candèze.

MATERIAL EXAMINED: E. insignitus (Lewis) (2)

Sadoganus Ohira, in Baba & Ohira, 1956:11. Type species: Sadoganus babai Ohira (by monotypy and original

designation).

Sadoganus is a monobasic Japanese genus (Kishii, 1987).

MATERIAL EXAMINED: S. babai Ohira (1, paratype)

Denticollinae: various tribes

All of the genera listed below have the ventral margin of the left mandible with a prominent notch immediately anterad the condyles. This notch is the ventral end of a prominent U-shaped groove also situated immediately anterad the condyles of the mandible. All taxa of Denticollinae sensu Stibick (1979) I have examined have this notch, but I do not know whether it should be considered diagnostic. A notch is also present in taxa belonging to the Pyrophorinae and the ampedine group of tribes in the Elaterinae (Ampedini, Megapenthini, Physorhinini). Further study is needed to determine the reliability of this character state.

Acroniopus Erichson, 1843:175, nomen novum for Atelopus Erichson, 1842, preoccupied by Atelopus Dumeril (Reptilia). Type species Atelopus humilis Erichson (designated by Hyslop, 1921:630).

Acroniopus is an Australian genus containing nine described species (Neboiss, 1956). Its affinities may be with Ascesis Candèze and its allies.

MATERIAL EXAMINED: A. humilis (Erichson) (4)

Anilicoides Candèze, 1895a:52. Type species: Anilicoides depressus Candèze (by monotypy).

Anilicoides is a monobasic genus from Australia (Schenkling, 1927); I have examined the type deposited in IRSNB. Like Acroniopus, its affinities may be with Ascesis.

MATERIAL EXAMINED: A. depressus Candèze (1, lectotype)

Anilicus Candèze, 1863, 328. Type species: Anilicus attenuatus Candèze (designated by Hyslop, 1921:627).

Anilicus contains five described species from Australia (Gullan, 1977); its affinities may also be with

Ascesis.

MATERIAL EXAMINED: A. attenuatus Candèze (1), A. semiflavus (Germ.) (2), A. parvus Gullan (1), A. xanthomus (W.S. Macleay) (1).

Ascesis Candèze, 1863:440. Type species: Ascesis australis Candèze (by monotypy).

Ascesis contains four described species from Australia (Neboiss, 1956). The configuration of the gena and mandibles around the condyles suggest Ascesis, Anilicus, Acroniopus, Anilicoides, Ochosternus and Dicteniophorus form a group of related genera.

MATERIAL EXAMINED: A. masteri (W. J. Macleay) (1)

Betarmonides Schwarz, 1906:147. Type species: Betarmon frontalis Sharp (designated by Hyslop, 1921:631).

Betarmonides is a genus of at least six described species from New Zealand (Schenkling, 1925).

MATERIAL EXAMINED: B. gracilipes (Sharp) (2)

Campylomorphus Jacquelin du Val, 1860:120. Type species Elater homalisinus Illiger (by monotypy).

This genus contains a single species from southwestern Europe. Leseigneur (1972:333) considers it "...l'un des ces geners enigmatiques dont les affinites difficiles à etablir". Specimens of C. homalisinus key to Denticollinae-Ctenicerini in Stibick (1979) and the overall habitus is similar to that of Ctenicera opacula (LeConte) from western North America. However, the larva attributed to this genus by Dolin (1978) would be highly unusual for any known denticolline. Known denticollines have abdominal segment IX flattened and notched apically. The larva illustrated by Dolin has abdominal segment IX rounded both in cross section and apically, like the known larvae of Sericosomini and some Elaterini (Jewett, 1946; Dolin, 1978; Costa & Casari-Chen, 1984). The striate impressions on tergum VIII and segment IX of Campylomorphus, which are lacking from known sericosomine and Elater group larvae, suggest a closer affinity to the Ampedini and Melanotini, though these striate impressions are present in some species of Agriotes (Ectinus) (Dolin, 1978). On the other hand, C.M.F. von Hayek (1990, pers. comm.) has advised that in her experience it is unwise to trust published larval-

adult associations unless one has reared the species oneself. Dolin apparently received the specimen illustrated from H.F. van Emden, and the justification for the association of the larva with Campylomorphus is unknown to me. On the basis of adult character states, I hereby transfer Campylomorphus to the Denticollinae, Ctenicerini.

MATERIAL EXAMINED: C. homalisinus (Ill.) (3)

Cardiorhinus Eschscholtz, 1829:34. Type species: Cardiorhinus seminiger Eschscholtz (designated by Hyslop, 1921:633).

The Cardiorhininae were synomymized with the Elaterini by Stibick (1979), but Cardiorhinus was treated as a member of the Denticollinae by Lawrence (1987). Cardiorhinus lacks the genal apomorphy of the Elaterini and has the mandibular characters discussed above for the Denticollinae. Its affinities may be with Hypodesis Latreille and Tomicephalus Latreille (q. v.). Cardiorhinus is a relatively large genus living in Central and South America; Schenkling (1927) lists 47 described species.

MATERIAL EXAMINED: C. seminiger Eschscholtz (3)

Dicteniophorus Candèze, 1863:441. Type species: Dicteniophorus fusiformis Candèze (designated by Hyslop, 1921:640).

Dicteniophorus is an Australian genus of 12 described species (Neboiss, 1956). Its affinities may be with Ascesis.

MATERIAL EXAMINED: D. melanoderus Candèze (2), D. fusiformis Candèze (1), D. ramifer (Eschscholtz) (1)

Heschatroxus Candèze, 1865:37. Type species: Heschatroxus holosericeus Candèze (by monotypy).

Heschatroxus includes at least three described species from Indonesia and New Guinea (Schenkling, 1925, as Eschatroxus).

MATERIAL EXAMINED: H. anticus Schwarz (1), H. rossi Fleutiaux (1)

Hypodesis Latreille, 1834:156. Type species: Hypodesis sericea Latreille (by monotypy).

The Hypodesinae were synonymized with the Elaterini by Stibick (1979), but Hypodesis was treated as a member of the Denticollinae by Lawrence (1987). Hypodesis lacks the genal apomorphy of the Elaterini and has the mandibular characters discussed above for the Denticollinae. Its affinities may be with Cardiorhinus and Tomicephalus. The genus contains at least nine described species living in Central America (Schenkling, 1927).

MATERIAL EXAMINED: H. vittata Candèze (1)

Ludigenus Candèze, 1863:325. Type species: Ludigenus politus Candèze (designated by Hyslop, 1921:653).

Ludigenus Candèze includes two described species from southeast Asia (Schenkling, 1927).

MATERIAL EXAMINED: L. politus Candèze (2)

Ochosternus Candèze 1863:445. Type species: Elater (Limonius) zealandicus White (designated by Hyslop, 1921:658).

Ochosternus contains at least 8 described species living in New Zealand and New Caledonia (Schenkling, 1927). Its affinities appear to be with the Australian genera allied to Ascesis (q. v.).

MATERIAL EXAMINED: O. zealandicus (White) (2)

Oxygonus LeConte, 1863:48. Type species: Elater obesus Say (by monotypy).

Oxygonus includes four North American species (Roache, 1963).

MATERIAL EXAMINED: O. obesus (Say) (6), O. montanus Schaeffer (2), O. ater Horn (1)

Paranilicus Candèze, 1878:191. Type species: Paranilicus macleayi Candèze (designated by Hyslop, 1921:662).

Paranilicus is an Australian genus containing two described species (Neboiss, 1956).

MATERIAL EXAMINED: P. macleayi Candèze (2)

Somomecus Solier, 1851:33. Type species: Somomecus parallelus Solier (by monotypy).

Somomecus is a monobasic genus from Chile.

MATERIAL EXAMINED: S. parallelus Solier (6)

Tomicephalus Latreille, 1834:146. Type species: Tomicephalus sanguinicollis Latreille (by monotypy).

The relationships of Tomicephalus are unknown. It shares with Hypodesis a glabrous and highly polished gena and the anterior margin of the frons elevated above the labrum for a distance about equal to the width of the labrum, and shares with both Hypodesis and Cardiorhinus a distinct groove on the ventral surface of the gena; the polarity of these characters is unknown. Schenkling (1927) lists eight species in this genus living collectively from Mexico to Ecuador and Brazil.

MATERIAL EXAMINED: T. sanguinicollis Latreille (1), T. abdominalis Candèze (1), T. bicolor Champion (2)

Pyrophorinae: various tribes

Anilicopsis Schwarz, 1907: 255, 284. Type species: Dicteniophorus dubius Schwarz, (by monotypy).

Anilicopsis dubius was described from Australia, but is believed to be based on a mislabelled specimen of Heligmus Candèze from South America (Neboiss, 1961).

MATERIAL EXAMINED: none

Candanius Hayek, 1973:85, nomen novum for Anius Candèze, 1889, preoccupied by Anius Pascoe, 1855 (Curculionidae). Type species: Anius gracillimus Candèze (by monotypy).

Candanius is a monobasic genus from Chile. Hayek (1973, as subfamily Agrypninae) transferred the name to the Agrypnini.

MATERIAL EXAMINED: C. gracillimus (Candèze) (1)

Idolus Desbrochers des Loges, 1875:42. Type species: Idolus breviusculus Desbrochers des Loges (by monotypy).

This genus was considered to be a member of the Pomachiliinae by Schenkling (1925), Méquignon (1930) and Leseigneur (1972) on the assumption that Athous picipennis Bach was the type species. However, A. picipennis was not one of the originally included species of Idolus and thus cannot be considered the type. Schwarz (1906) synonymized I. breviusculus and Elater bimaculatus Rossi, the type species of Drasterius Eschscholtz (Pyrophorinae, Conoderini). Idolus is thus a junior synonym of Drasterius. Specimens of Drasterius bimaculatus (Rossi) I have examined appear to be correctly placed in the Conoderini. The species assigned to Idolus by Schenkling, Mequignon and Leseigneur are now placed in Agriotella Brown.

MATERIAL EXAMINED: D. bimaculatus (Rossi) (3)

Nycterilampus Montrouzier, 1860:258. Type species: Nycterilampus lifuanus Montrouzier (by monotypy).

Nycterilampus is a genus of two described species from New Caledonia (Schenkling, 1927). The tarsal claws bear setae which place it within the Pyrophorinae according to Stibick (1979). Fleutiaux (1931a) lists Nycterilampus as a junior synonym of Tetrigus Candèze, which is also a member of the Pyrophorinae.

MATERIAL EXAMINED: N. velutinus Fleutiaux (2)

Scelisus Candèze, 1863: 283, 327. Type species: Scelisus sanguineus Candèze (by monotypy).

Scelisus was described for a single species from the Himalaya. Hayek (1973) synomymized this name and Lacon Laporte (Agrypnini).

MATERIAL EXAMINED: none

Thoramus Sharp, 1877:9. Type species: Thoramus wakefieldi Sharp (designated by Hyslop, 1921:672).

Thoramus is a New Zealand genus containing 11 described species (Schenkling, 1927). The tarsal claws bear setae, and Costa (1990) transferred the genus to the Pyrophorinae.

MATERIAL EXAMINED: T. wakefieldi Sharp (6)

Elaterinae: Ampedini/Megapenthini

Mecastrus Sharp, 1877:469. Type species: Mecastrus convexus Sharp (designated by Hyslop, 1921:655).

Mecastrus includes five described species living in New Zealand (Schenkling, 1927). It combines the character states used by Stibick (1979) to diagnose the Ampedini and Megapenthini. It shares with the Megapenthini a grooved prosternal mucro between the procoxae, and with the Ampedini, the entire elytral apices (as opposed to truncated or spined) and the broadly opened procoxal cavities (as opposed to constricted posteriorly). The Megapenthini are traditionally regarded as having the pronotosternal sutures unexcavated anteriorly; Mecastrus has unexcavated pronotosternal sutures. The Ampedini and Megapenthini are probably the least clearly diagnosed tribes in the Elaterinae and both may be repositories for genera of otherwise unknown placement.

MATERIAL EXAMINED: M. convexus Sharp (1)

Paranius Champion, 1895:404. Type species: Paranius mexicanus Champion (by monotypy).

Paranius is a monobasic Mexican genus. Specimens of P. mexicanus received from the Canadian National Collection of Insects, Ottawa, bore labels stating Paranius is a synonym of Megapenthes Kiesenwetter, but to the best of my knowledge, this has not been published.

MATERIAL EXAMINED: P. mexicanus Champion (4)

Psiloniscus Candèze 1860:3. Type species: Psiloniscus sticticus Candèze (by Hyslop, 1921:677).

Psiloniscus is a genus of at least five Central American species (Schenkling, 1925).

MATERIAL EXAMINED: P. sticticus Candèze (3), P. brunneus Candèze (1), P. borborurus Candèze (1)

Smiliceroides Schwarz, 1906:138. Type species: Smiliceroides quadrilineatus Schwarz (by monotypy).

Smiliceroides is a monobasic genus from Mexico. The partially closed procoxal cavities and bidentate elytral apices place it more or less within Stibick's (1979) concept of Megapenthini. However, like Psiloniscus, the prosternal mucro is grooved posterad the procoxae but not between them as stated in Stibick's key.

MATERIAL EXAMINED: S. quadrilineatus Schwarz (syntype)

Elaterinae: Physorhinini

Monelasmus Candèze, 1863:332. Type species: Monelasmus guyanensis Candèze (designated by Hyslop, 1921:657).

This genus is monobasic, the other three species included by Candèze having been transfered to Anchastus LeConte (Elaterinae, Physorhinini) by Champion (1895). I have examined the holotype of M. guyanensis deposited in NHM, London. It is similar to specimens of Anchastus moratus Candèze from Panama identified by Arnett in the Smithsonian Institution. On this basis, Monelasmus is here transfered to the Physorhinini. M. guyanensis lives in northern South America.

MATERIAL EXAMINED: M. guyanensis Candèze (1, type)

Pomachilioides Candèze, 1897:51. Type species: Pomachilioides ludiiformis Candèze (by monotypy).

Pomachilioides contains two described species from Sumatra (Schenkling, 1927). I have examined the type of P. ludiiformis deposited in IRSNB. It shares with the Physorhinini the lobed third tarsomere and complete frontal carina, and shares with Physorhinus the yellow frons and apical pallisade of spines on the hind tibia.

MATERIAL EXAMINED: P. ludiiformis Candèze (1, syntype)

Oestodinae

Anaspasis Candèze, 1881:4. Type species: Anaspasis fasciolata Candèze (= Deromecus parallelus Solier) (by monotypy).

Anaspasis includes three described species living in Chile (Schenkling, 1925). It was allied with Protelater Sharp by Fleutiaux (1941), and placed in the Oestodini by

Stibick (1979).

MATERIAL EXAMINED: A. parallelus (Solier) (3)

Protelater Sharp, 1877:33. Type species: Protelater elongatus Sharp (designated by Hyslop, 1921:667).

Protelater includes at least 12 described species living in New Zealand (Schenkling, 1925). Stibick (1979) placed it in the Oestodini.

MATERIAL EXAMINED: P. viticollis Broun (1)

Sphaenelater Schwarz, 1902:365. Type species: Sphaenelater nigricornis Schwarz (by monotypy).

Sphaenelater contains five described species, all living in New Zealand (Schenkling, 1927, as Geranus Sharp). Stibick (1979) placed this genus in his tribe Sphaenelaterini.

MATERIAL EXAMINED: S. lineicollis (White) (3)

Incertae sedis

Compshelus Candèze, 1878:48. Type species: Compshelus flavus Candèze (by monotypy).

Compshelus is a monobasic genus from Fiji; its affinities are a mystery to me.

MATERIAL EXAMINED: C. flavus Candèze (lectotype, 8 non-types)

Doloporus Candèze, 1887:289. Type species: Doloporus aterrimus Candèze (designated by Hylsop, 1921:641).

Doloporus is an Australian genus containing two described species (Neboiss, 1956). I have seen a specimen of D. aterrimus in the California Academy of Sciences, but did not come to a conclusion about its affinities.

MATERIAL EXAMINED: D. aterrimus Candèze (1)

TAXA OF UNKNOWN STATUS

The following taxa have been assigned to either the Elaterini, Pomachiliini or Adrastini as traditionally defined. I have not been able to examine specimens representing these genera, and their status is unknown.

Aphanopenthes Fleutiaux, 1932: 35. Type species: Aphanobius acutipennis Germar (designated by Arnett, 1955:603).

Aphanopenthes was proposed for three species from the Mascarene Islands east of Madagascar that had been placed in Aphanobius. Fleutiaux (1932) compared Aphanopenthes with Aphanobius.

Caldeonius Candèze, 1895b:67. Type species: Caldeonius suturalis Candèze (by monotypy).

This genus was proposed for one species from Madagascar with bidentate tarsal claws. The type of C. suturalis is deposited in IRSNB, Brussels, but has been out on loan for the duration of this study.

Chesotraxus Fleutiaux, 1940b: 98. Type species: Chesotraxus celebensis Fleutiaux (by original designation)

Chesotraxus was proposed for two species from Indonesia and Philippines. Fleutiaux (1940b) believes it is similar to Heschatroxus Candèze, a genus I have excluded from the Elaterini.

Dulius Fleutiaux, 1906:199. Type species: Dulius aberrans Fleutiaux (by monotypy).

Dulius was proposed for a single species from Madagascar. Fleutiaux (1906) remarks only, "A tout á fait l'aspect d'un Ludius [=Elater], mais la conformation du front le place parmi les Pomachilides."

Hoabinh Fleutiaux, 1940a:195. Type species Hoabinh coomani Fleutiaux (by monotypy).

Hoabinh was proposed for a single species from Vietnam. Fleutiaux (1940a) compares it with Neotrichophorus.

Idiotarmon Binaghi, 1940: 101. Type species: Betarmon quadrivittatus Ragusa (by original designation and monotypy).

Idiotarmon was proposed for a single species from Italy. Little appears to be known about the type species (Platia & Bartolozzi, 1988). Schenkling (1925) lists the type species as a synonym of Betarmon anatolicus Candèze, the type species of Idiotarmonides Agajev, below.

Idiotarmonides Agajev, 1985: 66. Type species: Betarmon anatolicus Candèze (by original designation?).

I know little about this name. The genus contains two species (Platia & Schimmel, 1992).

Lanecarus Ohira, 1962a:199. Type species: Agriotes palustris Lewis (by original designation).

I know little about this genus. According to Kishii (1987), it is a traditional adrastine with tarsomere 3 lobed. His diagnosis of the genus suggests species of Synaptus. Two species are known from Japan (Kishii, 1987), two are described from Borneo (Ohira, 1973a), and two Chinese species were transferred to Lanecarus from Silesis by Platia & Schimmel (1991a). Hayek (1990) distinguishes Lanecarus from Adrastus by the structure of the mesocoxal cavity. From what I can see of the gena in fig. 59 of Hayek (1990), Lanecarus is probably a member of the Elaterini.

Neosilesis Ohira, 1973a:135. Type species: Neosilesis borneoensis Ohira (by original designation and monotypy).

This genus was proposed for a single species from Borneo. Some structures are illustrated by Hayek (1990).

Parabetarmon Ohira, 1970:106. Type species: Neotrichophorus carinicephalus Miwa (by original designation and monotypy).

This genus was proposed for a single species from Japan. Kishii (1987) provides a diagnosis.

Paraupenthes Ohira, 1971:298. Type species: Megapenthes subinconditus Van Zwaluwenburg (by original

designation and monotypy).

Paraupenthes was proposed for a single species from Micronesia in the west Pacific Ocean. Ohira (1971) believed it to be somewhat related to Parabetarmon from southern Japan and Taiwan.

Pseudonomopleus Fleutiaux, 1931b:29. Type species: Pleonomus niger Candèze (by original designation).

This genus was proposed for two species from southern Africa. "Se place dans le voisinage immédiat de Doloporus E. Candèze" (Fleutiaux, 1931b:30).

Shirozulus Ohira, 1966:270. Type species: Shirozulus formosanus Ohira (by original designation).

Shirozulus was proposed for two species, the type species from Taiwan and another species from Japan. Ohira (1966) believed it to be closely related to Vuilletus, a genus I have placed tentatively in the Sericosomini. Kishii (1987) placed the Japanese species (S. bifoveolatus) in Sericus without mentioning Shirozulus; the specimen of this species I have examined belongs to the Sericosomini (see Sericus above).

Stibadoderus Burmeister, 1875:271. Type species: Stibadoderus murinus Burmeister (by monotypy).

This genus was proposed for a single species from Argentina. According to the key to Pomachiliini in Schwarz (1906), it appears to be characterized by a lack of distinctive characters.

Tolphorea Guryeva, 1983:81. Type species: Tolphorea volans Guryeva (by monotypy).

I know little about this genus. Two species, both apparently from Iran, are included in it by Platia & Schimmel (1993a).

EVOLUTIONARY CONSIDERATIONS

This section deals with the relationships among the genera of Elaterini based on hypotheses of reconstructed phylogeny. The hypothesized phylogeny is reconstructed using structural characters of the Elaterini and its proposed outgroup, the Sericosomini. Biogeographical implications of the reconstructed phylogeny also are discussed.

Cladistic methods proposed by Hennig (1966) were used to elucidate postulated relationships within the Elaterini. Literature on this subject has become voluminous and diverse and it is not my intention to summarize it here. For an excellent recent treatment I recommend Ax (1987). Commonly used procedures are summarized by Wiley et al. (1991). Since the character states described below are strictly structural, I use the more restricted terms plesiomorphic and apomorphic rather than the more inclusive plesiotypic and apotypic to describe character state polarities. Character state polarities were determined by the outgroup comparison methods of Watrous and Wheeler (1981) and Maddison et al. (1984).

Taxa Studied

Taxa in which character states were examined are listed under each genus in the 'Classification of the Elaterini' and 'Genera Excluded from the Elaterini' above.

Monophyly of the Elaterini + Sericosomini

As discussed in the 'Structural Features of Elaterini' and 'Genera Excluded from Elaterini' above, genera I include in the Elaterini and Sericosomini have the ventral margin of the gena divergent anteriorly from the ventral margin of the eye (Figs. 1B, C) with the apex of the gena below the mandible produced anteriorly. I interpret this as a synapomorphy uniting these two tribes. All other genera of Elaterinae I have examined have the ventral margin of the gena subparallel with the ventral margin of the eye (Fig. 1A), with the apex not or little produced.

Monophyly of the Elaterini

All the genera I include in the Elaterini have the following two autapomorphic character states: apex of the anterior margin of the gena produced distinctly anterad the ventral condyle of the mandible, with the gena lacking a complete submarginal carina (Fig. 1C); ventral condyle of the mandible situated distinctly anterad the level of the dorsal mandibular condyle (Fig. 3B). For initial inclusion

of taxa, only the first character was used since it is clearly visible externally.

Phylogenetic Designation of Character States

The characters listed below were selected from those discussed in the 'Structural Features of Elaterini' above, based on my ability to non-arbitrarily define and confidently polarize the character states. All characters, except character 36, were polarized by outgroup comparison. A data matrix was compiled for the 37 characters discussed below and 32 taxa of Elaterini for which adequate data were available (Table 2). Agriotella and Cosmesus were treated as a single taxon in the data matrix since their character states did not differ. Characters are presented in the order they first appear in the consensus cladogram (Fig. 12).

1. **Anteroventral margin of gena.** Two states: plesiomorphic (0), divided by mandible (Fig. 1B); apomorphic (1), undivided by mandible (Fig. 1C).
2. **Position of ventral condyle of mandible relative to dorsal condyle.** Two states: plesiomorphic (0), ventral condyle roughly aligned dorsoventrally with dorsal condyle (Fig. 3A); apomorphic (1), ventral condyle situated more anterad than dorsal condyle (Fig. 3B).
3. **Anterior articulating surface of mesosternum.** Two states: plesiomorphic (0), ventral (Fig. 8D); apomorphic (1), anterior (Fig. 8C).
4. **Number of accessory glands of bursa copulatrix.** Three states: plesiomorphic (0), none; apomorphic (state 1), one (Fig. 11C); apomorphic (state 2), two (Fig. 11D).
5. **Mesal margin of prothoracic hypomeron.** Two states: plesiomorphic (0), with impunctate border (Fig. 5F); apomorphic (1), without impunctate border (Fig. 5E).
6. **Lateral lobes of mesosternum.** Two states: plesiomorphic (0), uniformly concave or "flat" (Fig. 8C); apomorphic (1), with a conspicuous secondary depression (Figs. 8B, E).
7. **Shape of colleterial glands.** Two states: plesiomorphic (0), globular (Fig. 11C); apomorphic (1), elongate (Fig. 11A).

   Chiagosnius (Sericosomini) has the derived condition.
8. **Apicolateral groove on right mandible.** Two states: plesiomorphic (0), indistinct: left and right mandibles more symmetrical (Fig. 3E); apomorphic (1), distinct: left and right mandibles quite asymmetrical (Figs. 3F-H).

   This character state is not consistent within the New World species of Neotrichophorus. Neotrichophorus depressus (Champion) from Central America has the ancestral condition, while the species of Neotrichophorus from the southern Nearctic region have the derived condition. See

Neotrichophorus in 'Classification'. Data for the data matrix were taken from the latter group.

9. **Pit on lateral margin of left mandible.** Two states: plesiomorphic (0), absent; apomorphic (1), present.

This character is not consistent within the New World species of Neotrichophorus. Neotrichophorus depressus (Champion) from Central America has the ancestral condition, while the species of Neotrichophorus from the southern Nearctic region have the derived condition. See Neotrichophorus in 'Classification'.

10. **Internal anterolateral projection of prosternum, anterior aspect.** Two states: plesiomorphic (0), elongate dorsally (Fig. 4H); apomorphic (1), flattened (Fig. 4G).

11. **Epipharyngeal bar sclerites, horizontal length.** Two states: plesiomorphic (0), short horizontally, distinctly separated medially (Fig. 2A); apomorphic (1), long horizontally, strongly arched basally, much less separated medially (Fig. 3E).

12. **Spiracular sclerite of segment VIII, posterior margin.** Two states: plesiomorphic (0), absent or indistinct; apomorphic (1), distinct (Fig. 10K).

13. **Bursa copulatrix.** Five states: plesiomorphic (0), more or less linear, spermathecal duct anterior (Fig. 11A); apomorphic (state 1), distinctly coiled, spermathecal duct anterior (Fig. 11B); apomorphic (state 2), recurved, spermathecal duct posterior, accessory gland anterior (Fig. 11D); apomorphic (state 3), recurved, spermathecal gland posterior, anterior accessory gland absent (Fig. 11E); apomorphic (state 4), secondarily linear, spermathecal gland usually posterior.

State 1 and state 2 are interpreted as arising independently from the ancestral state. States 3 and 4 are interpreted as further modifications of state 2. Agriotes (sensu stricto) and Agriotes (Ectinus) are coded '0' on the basis of the type species.

14. **Crest between apicolateral groove and ventral margin, right mandible.** Two states: plesiomorphic (0), absent (Fig. 3E); apomorphic (1), present (Fig. 4A).

15. **Anterior margin of basal expansion of left mandible, dorsal aspect.** Two states: plesiomorphic (0), more oblique (directed anteroventrally) (Fig. 4B); apomorphic (1), more perpendicular (directed ventrally) (Fig. 4C).

The derived condition appears to be homoplastic within the subfamily Elaterinae. A relatively perpendicular anterior margin of the basal expansion on the left mandible is also seen in Physorhinus and Anchastus (Physorhinini), Dicrepidius and Dipropus (Dicrepidiini) and in the Longicornis group of Megapenthes (Megapenthini).

16. **Distance from apex of apical part of gonocoxites to base of stylus of ovipositor.** Two states: plesiomorphic (0), much less than length of stylus (Fig. 10H); apomorphic (1), at least half the length of stylus (Fig. 10I).

It is entirely possible that the polarity of this character could be reversed. If the subapical position of the stylus is a modification associated with oviposition in harder substrates, it could be an ancestral character state (see discussion of strengthening of ovipositor in 'Reconstructed Character Evolution', below).

17. **Terebral tooth of right mandible, occlusal aspect.** Two states: plesiomorphic (0), relatively small (Fig. 3C); apomorphic (1), relatively large (Fig. 3D).

This character is homoplastic both in the Elateridae and in the Sericosomini. A relatively large terebral tooth is present in Chiagosnius, Melanotus (Melanotinae) and some species of Megapenthes (Elaterinae: Megapenthini). It is possible that the polarity of this character for the family is the opposite of the interpretation presented above.

18. **Epipharyngeal bar sclerites, anterior-posterior length.** Two states: plesiomorphic (0), relatively short antero-posteriorly: extended posteriorly less than median width of labrum (Fig. 2A); apomorphic (1), relatively long antero-posteriorly: extended posteriorly distance about subequal to median width of labrum (Fig. 2F).

The ancestral state is present in only some genera of the outgroup; the derived condition is present in Chiagosnius.

19. **Basistipes.** Two states: plesiomorphic (0), more than 1 long seta present in basal half (Fig. 4D); apomorphic (1), only one long seta in central area (Fig. 4E).

This character is homoplastic within the Elateridae. The derived state is also present in Dolerosomus and possibly Cardiophorus.

20. **Armature of bursa copulatrix.** Three states: plesiomorphic (0), spines more or less uniformly distributed or forming rows (Fig. 11C); apomorphic (state 1), pair of dorsal-ventral fans of spines (Fig. 11E); apomorphic (state 2), spiny plates (Fig. 11F).

In Sericus, the bursa bears a small unspined plate. In Chiagosnius and Dolerosomus, the bursa has spines forming rows. In all but two taxa of Elaterini, as well as almost all species of Elateridae I have examined, either spines or spiny plates are present on the bursa. Since I believe spiny plates can be easily derived from clusters of spines, I interpret the presence of spines on the bursa as the ancestral condition for the Elaterini.

Adrastus and the Sparsus group of Agriotes lack bursal armature. In all preliminary analyses, the Sparsus group appeared as the sister group of the Sputator group of Agriotes and not as the sister group of Adrastus. I concluded that including the Sparsus group was uninformative, and it was removed from the data matrix. This rendered the lack of bursal armature autapomorphic for Adrastus, and created a 'non-applicable' character state in

the data matrix. Since the computer program I have used for phylogenetic calculations does not appear to distinguish between 'missing' and 'non-applicable' character states, Adrastus has been coded as ancestral. Agriotes (sensu stricto) and Agriotes (Ectinus) are coded as state 2.

Lack of bursal armature is homoplastic within the Elateridae. In Hypnoidus Dillwyn (Denticollinae: Hypnoidini), the bursa copulatrix lacks either spines or plates.

21. **Subpronotal lobe of prothorax.** Two states: plesiomorphic (0), emargination of lobe shallow, curved (Fig. 4G); apomorphic (1), emargination of lobe deep, subquadrate (Fig. 4I).

22. **Apical stout setae of hind angles of pronotum.** Two states: plesiomorphic (0), directed posterolaterally, usually long (Fig. 5G); apomorphic (1), directed posteriorly, short.

23. **Mesotrochantin.** Three states: plesiomorphic (0), ca. twice as long as wide at median in ventral aspect (Fig. 8C); apomorphic (state 1), ca. as long as wide in ventral aspect (Fig. 8D); apomorphic (state 2), concealed: not visible in ventral aspect (Fig. 8A).

I interpret these three states as a transformation series characterized by a reduction in size of the mesotrochantin. A visible but roughly subquadrate mesotrochantin is interpreted here as intermediate between a subrectangular mesotrochantin and a concealed mesotrochantin.

24. **Margin of mesosternal fossa.** Two states: plesiomorphic (0), not beaded (Fig. 7C); apomorphic (1), raised, thin, beaded (Fig. 7D).

25. **Internal anterolateral margin of prosternum, ventral aspect.** Two states: plesiomorphic (0), not visible, or visible and truncate, not prominent (Fig. 5E); apomorphic (1), visible, acute or rounded, prominent (Fig. 5F).

26. **Frontal carina.** Two states: plesiomorphic (0), incomplete (Fig. 1G); apomorphic (1), complete, separate from anterior margin of frons (Fig. 1D).

Formulating a transformation series for this character within the Elaterini is difficult, since the complete frontal carina appears in three different configurations, as discussed above in 'Structural Features of Elaterini'. I cannot visualize any one of the configurations being intermediate between the other two. Complicating the problem are the Criddlei group of Agriotes, Mesembria and the Cognatus group of Dalopius. The Criddlei group is a problematic pair of species whose systematic position is disputed. North American authors follow Becker (1956) and place the group in Agriotes, but Guryeva (1972) has placed the group in Dalopius Eschscholtz. The Cognatus group may not be congeneric with the type species of Dalopius. In

the type species of Agriotes and Dalopius, the frontal carina is incomplete and the supraantennal crests are directed ventrally. In the Criddlei group, Mesembria and the Cognatus group the frontal carina is incomplete, but the supraantennal crests are directed mesally, towards the midpoint of the anterior margin of the frons. In some individuals of Agriotes criddlei Van Dyke, Dalopius cognatus Brown and some species of Mesembria, the supraantennal crests are very narrowly separated (by one puncture in some specimens), approaching the configuration of the frontal carina in Agriotella. Based on the observed configurations, derivation of a complete frontal carina in Agriotella from an A. criddlei/D. cognatus/Mesembria-like ancestor seems a more plausible hypothesis than derivation de novo or via an ancestor with an established complete frontal carina. As far as Ypsilostethus is concerned, I have no reason to believe, on the basis of the observed configurations, that derivation of a Pomachilius-like frontal carina from an Ypsilostethus-like ancestor is more plausible than the reverse.

In the data matrix, the frontal carina is coded simply as complete or incomplete, since I am uncertain of the transformation series. The frontal carina of Glyphonyx is various but is traditionally regarded as complete, presumably based on the type species; it is coded as such in the data matrix.

27. **Lateral carina of pronotum.** Two states: plesiomorphic (0), meeting anterior margin of pronotum dorsad mesal margin of hypomeron (Fig. 5D); apomorphic (1), meeting anterior margin of pronotum at same point as mesal margin of hypomeron (Fig. 5B).

28, 29. **Tarsomeres 4 and 3, respectively.** Two states: plesiomorphic (0), unlobed (Fig. 10A); apomorphic (1), lobed (Figs. 10B, C).

The fossil record suggests the presence of lobes on tarsomeres 3 and 4 is the ancestral condition for Glyphonyx. Species of Glyphonyx from Chiapan amber of Oligocene-Miocene age from Mexico have both tarsomeres 3 and 4 lobed (Becker, 1963; Zaragoza Caballero, 1990), as does a species of Glyphonyx in my collection from Dominican amber. Dominican amber is thought to be no older than Miocene in age, but is known to be of various ages and some specimens are Recent (B.V. Brown, pers. comm.). As noted above, present day New World species of Glyphonyx have only tarsomere 4 lobed. Since the type species is a New World species, Glyphonyx is coded as ancestral for character 29 and derived for character 28.

30. **Basal face of mandibles.** Three states: plesiomorphic (0), without pronounced tooth or flange (Fig. 3D); apomorphic (state 1), with pronounced flange (Fig. 3J); apomorphic (state 2), with pronounced tooth (Fig. 3I).

The flange of state 1 is also present in Chiaqosnius.

Some other taxa bear a much less distinct flange along the ventral margin of the contact zone. I propose that the small ventral flange has become enlarged ventrally and reduced posteriorly in Synaptus, and then further reduced posteriorly until only an anteroventral tooth remains in Adrastus, Ctenoplus, Glyphonyx, Parasilesis, Peripontius and Silesis. The large anteroventral flange is interpreted here as an autapomorphy for Synaptus, and the anteroventral tooth as an apomorphy uniting the other six genera.

31. **Tooth/flange of basal face of mandible.** Two states: plesiomorphic (0), in same plane as rest of basal face; apomorphic (1), directed occlusally (Fig. 3K).

32. **Epipharyngeal bar sclerites, anterior divergence.** Two states: plesiomorphic (0), divergent anteriorly for about three-quarters of length (Fig. 2F); apomorphic (1), subparallel posteriorly for about one-half of length (Fig. 2G).

33. **Procoxal cavities.** Two states: plesiomorphic (0), open dorsally (Fig. 7a); apomorphic (1), closed dorsally by proendosternite (Fig. 7B).

This character is homoplastic in the Elateridae. The procoxal cavities are closed dorsally in Anchastus cinereipennis (Eschscholtz) (Elaterinae, Physorhinini).

34. **Tarsal claws.** Three states: plesiomorphic (0), simple (Fig. 10E); apomorphic (state 1), pectinate (Fig. 10G); apomorphic (state 2), flanged (Fig. 10F).

A transformation series deriving state 2 from state 1 is not proposed for this character. The flanged tarsal claw is interpreted here as an autapomorphy for Ypsilostethus. Both of the apomorphic character states are homoplastic within the Elateridae (and Coleoptera in general). Flanged tarsal claws are present in at least the Cardiophorinae (Horistonotus Candèze, Esthesopus Eschscholtz) and Negastriinae (Oedostethus LeConte). Pectinate tarsal claws are present in at least the Cardiophorinae (Aptopus Eschscholtz) and Melanotinae (all genera; see Hayek, 1990).

35. **Periocular pits.** Three states: plesiomorphic (0), periocular space variously grooved between supraantennal crest and gena (Fig. 1H); apomorphic (state 1), periocular pits irregularly shaped, relatively shallow (Fig. 1J); apomorphic (state 2), periocular pits deep, subcircular (Fig. 1I).

36. **Spiny plates of bursa copulatrix.** Two states: plesiomorphic (0), rounded (Fig. 11F); apomorphic (1), conspicuously attenuated posteriorly (Fig. 11G). Basis for postulate: functional outgroup comparison.

In some taxa with the dorsal-ventral fans of spines, the bases of the spines have fused to form a rounded plate. For this reason, I interpret a rounded bursa plate as the ancestral state for this character.

37. **Metasternal sulcus.** Three states: plesiomorphic (0), present and grooved for at least 2/3 length of sternum

(Fig. 9A); apomorphic (state 1), present but reduced anteriorly (Fig. 9B); apomorphic (state 2), absent (Fig. 9C).

I interpret these character states as a transformation series in which the metasternal suture is reduced anteriorly (state 1) in Parasilesis and then lost entirely in the other four taxa (state 2).

Calculation of the Reconstructed Phylogeny

It was apparent during compilation of the data matrix that considerable homoplasy and character conflict are present in the data. Phylogenetic analysis was performed using the HENNIG86 computer algorithm (Farris, 1988). An attempt was made to find the shortest possible tree(s) using the implicit enumeration (ie) command. According to Farris (1988), this command produces trees which are "certain to be of minimal length, but the calculation may be time-consuming if there are many terminals or much incongruence". This command was found to be prohibitively time-consuming for my data matrix, and I opted for the 'mhennig*' plus 'bb*' commands. Farris (1988) recommends using this combination of commands for large or complex data matrices. The 'mhennig*' command "constructs several trees, each by a single pass, adding terminals in several different sequences" (Farris, 1988), retaining the shortest trees, and then applies branch-swapping to each of the initial trees. The subsequent 'bb*' command applies extended branch-swapping to the tree(s) produced by the 'mhennig*' command, using all available memory if necessary to store the shortest trees found (Farris, 1988).

Initially 'mhennig*' alone was used to search for hidden topologies in the data matrix. The data matrix was randomly rearranged into 10 different arrangements of taxa (although the outgroup was kept as the first taxon), and analyzed using 'mhennig*'. The resulting trees differed in details, but not in overall topology. In these analyses, no more than two trees of shortest length (110 steps) were produced. The data matrix with taxa in alphabetical order was then analysed using the 'mhennig*' plus 'bb*' combination. This calculation found 18 trees of 110 steps, with a consistency index of 0.42 and a retention index of 0.80. A Nelson consensus tree calculated using the 'nelsen' command is shown in Fig. 12. The 18 trees are combinations of various resolutions of the polychotomies in the consensus tree. The resolutions of these polychotomies are shown in Figs. 13-19.

The reconstructed phylogeny presented in Fig. 12 is the most parsimonius for the available data, and considering the homoplasy and character conflict apparent

in the data matrix, the topology seems a reasonable approximation of the evolution of the Elaterini. However, I am unconvinced Ypsilostethus and Mesembria are sister groups. Mesembria is one of the taxa for which specimens were unavailable for disarticulation; the states of 10 of 37 characters in Table 1 are unknown. I believe the sequential evolution of Agelasinus, then Ypsilostethus, then Mesembria is more plausible than the most parsimonious solution calculated by HENNIG86. This scenario does not require the independent evolution of the crenellated margin of the mesosternal fossa (character 24) in Mesembria and Ancestor L. This character state is unique in the Elateridae and I believe it has arisen only once.

I am unconvinced also by the transformation series of the periocular pits (character 35) implied by the placement of Ctenoplus in a polychotomy arising from Ancestor U. Under this scenario, a transformation series of state 0 > state 2 > state 1 is proposed. This does not seem apparent in the character configurations (Figs. 1H-J). The periocular pits of Ctenoplus (Fig. 1J) seem to represent a simple partial closure of the groove in Fig. 1H, rather than a reduction of the pits in Fig. 1I. Like the crenellated margin of the mesosternal fossa, the deep, subcircular periocular pits are unique in the Elateridae, and I believe they have arisen only once. However, weighting this character as high as possible in HENNIG86 analyses did not change the topology in Fig. 12, or the alternatives in Figs. 18 and 19.

Reconstructed Character Evolution

Since the pattern of character evolution in Figs. 12-19 is complicated by homoplasy and reversal, the pattern of evolution for each character is summarized in Table 3.

The overall evolutionary pattern is relatively simple in that, for most characters, there is no subsequent specialization of the apomorphic state. However, much independent evolution of apomorphic states and reversal to ancestral states is required by the reconstructed phylogeny. Of the 46 apomorphic character states, only 11 show no homoplasy. Depending on the resolutions of the polychotomies in Fig. 12, either 99 or 105 changes in state (appearance of an apomorphic state or reversal to an ancestral state) occur in the 46 apomorphic states.

One of the most complicated patterns is in character 12 (posterior margin of spiracular sclerite of abdominal segment VIII). The apomorphic state appears in Ancestors D and F, is subsequently lost in Leptoschema and Ancestor I, reappears in Deromecus and Ancestor R, and is lost again in

Ancestor U, for a total of 7 changes in state. The functional significance of this character is unclear, and possibly it is randomly appearing and disappearing by mutation. Perhaps the metabolic cost of producing it does not significantly affect survival or its presence does not significantly affect reproductive success, and thus there is no significant selection pressure against this character.

The evolution of character states is not merely an abstraction suitable for manipulation by an algorithm designed to produce a statement of logic rather than an hypothesis of phylogeny. Rather, as argued by Shpeley & Ball (1993), character state changes occur in living organisms and as such must be regarded as changes that either enhance, or at least do not significantly hinder, the ability of an organism to survive in the habitat it occupies and reproduce successfully. While it is frequently impossible to determine with certainty the significance of a modification, the following speculations are presented in the above context.

The modification of structural features in adult Elaterini must occur within two severe evolutionary constraints. First, any modification must either enhance, or not impair, the effective functioning of the startle/escape mechanism of the click beetle's "click". Second, any modification must either enhance, or not hinder, the ability of adults to escape the larval habitat. In regard to the first constraint, the "click" mechanism of Elateridae represents a significant evolutionary investment in terms of muscle mass and structural modification of the pro- and mesothorax, and must represent a response to a significant selective force affecting survival. With regard to the second constraint, adults and larvae of Elaterini (and all other Elateridae of which I am aware) occupy quite different habitats. Adults are free living and must search for mates. Known larvae of Elaterini live in rotten wood, leaf litter and soil. Failure of an adult to escape the larval habitat will significantly affect its reproductive success.

The "jump" or "click" of elaterids is described by Evans (1972). The most conspicuous structures involved in the "jump" are the prosternal mucro and the mesosternal fossa. Briefly descibed, the "jump" is produced by hooking the posterodorsal end of the mucro into the notch at the anterior end of the fossa (between the anterior articulating surfaces; Fig. 8A), and maintaining the hold by friction while tension is built up in a pair of muscles that occupy most of the body cavity of the prothorax. The friction hold may be released by depressing the anterior

end of the prosternum. Once released, muscle tension forces the mucro into the fossa very rapidly (in less than 1 millisecond). The sound of the "click" is produced when the posterior margin of the prosternum and hypomeron strike the anterior margin of the mesosternum and mesepisternum.

In most references to the "jump" of elaterids, the function of the "jump" is described as an ingenious method the beetle has for righting itself should it find itself lying on its back (dorsal surface). While the "jump" certainly accomplishes this, it is an unlikely evolutionary driving force for an event that is rarely, if ever, encountered (except when curious people are present!), and for which adequate mechanisms for turning over already exist (e.g., flexing the elytra, anchoring and pulling with the tarsal claws). It also does not explain why elaterids can "jump" from either the dorsal or ventral surface. It is more probable that the "jump" is a combination startle/escape mechanism, as suggested by Hyslop (1915). I have seen some species of Cardiophorinae and Negastriinae "jump" when approached. Negastriines 2-3mm in length living under rocks by creeks will "jump" 10-20cm away when the rock is lifted - apparently large elateridologists are perceived as a threat! However, the much more common reaction to threat is to tuck in the appendages and drop from the object the beetle is on, relying more on crypsis than the "jump" mechanism. The "jump" then is used if the threat persists. Personal experience with trying to pick up live elaterids with watchmakers forceps (not recommended) and fingers has shown that the "click" can easily dislodge the beetle from your grasp. Watchmaker forceps can be viewed as a rough approximation of the beak of a bird. Thomas (1940) considered birds to be the the most important predators of click beetles.

From Figs. 6A-E, it can be seen that the dorsal surface of the prosternal mucro, the surface involved in the "jump" mechanism, has remained relatively unmodified, while the ventral surface shows considerable variation. From Figs. 7A-F, it can be seen that the anterior and inner surfaces of the fossa have remained relatively unmodified, but the margins of the fossa and the lateral lobes of the mesosternum show considerable modification. No structures have been modified that would impair the effectiveness of the "jump" mechanism.

While the character states of the ventral surface of the mucro have not been used in reconstructing the phylogeny of the Elaterini, they may be important characters for diagnosing monophyletic groups within the Elaterini when more information is obtained. Viewed in isolation, the modifications of the ventral surface of the

mucro and margins of the mesosternal fossa seem to have little significance. However, viewed in context of the action of the mucro during the "jump", these modifications can be viewed as wedges or pinchers that can be used against the beak of a bird grabbing the body transversely across the mesothorax.

The body outline of adult Elaterini is remarkably smooth: few depressions, flat surfaces or protuberances that can be used to get a good grip are present. As noted above, elaterids are very difficult to pick up with thin, pointed objects. However, the mesothorax appears to be a significant weak point. The dorsal surface of the body bears a conspicuous depression on the mesonotum to accomodate the posterior margin of the pronotum when the mucro is raised out of the mesosternal fossa. This depresssion is protected in Elaterini by the elongated hind angles of the pronotum and the raised carina of the hind angles. Elongated and carinate hind angles are present in many, but not all, Elateridae. Likewise, the mesosternum is relatively flat and bounded posteriorly by raised mesocoxae, but is protected in Elaterini by the raised margins of the mesosternal fossa. A bird grabbing an elaterid around the mesothorax, finds its beak resting precariously, both dorsally and ventrally, on a pair of sharp, parallel ridges, rather than on a flat surface. When the friction hold on the mesosternum is released, the mucro, being too high to slide under the beak, strikes the beak, suddenly and with considerable force. The startle effect alone could be enough to cause the bird to drop the beetle, or more likely, the transfer of momentum could cause the beetle to slide along the sharp ridges, out of the bird's grasp. In taxa with a sloping or horizontal ventral surface of the mucro (Figs. 6A, B), dislodgement could be aided by the force of the mucro prying open the beak. In taxa with an abrupt subapical tooth (Figs, 6C, D), the force of the mucro stiking the beak may be the sole means of dislodgement.

In general terms, this is how I believe the "jump" mechanism has evolved. The specifics, as usual, are undoubtably more complicated. Significant variance in the shape of the margins of the mesosternal fossa are present, though the margins of the fossa are elevated at least to the level of the ventral surface of the mesocoxae. The significance of the crenellated fossal margin (character 24, Fig. 7D) is unclear. It is present in taxa with relatively smaller body size than most of those without the crenellated margin, and may have some significance when dealing with smaller-sized predators. Secondary depressions (character 6, Figs. 8B, E) have evolved independently four times (Table 2); functionally these

could serve to break up the otherwise flat surface of the mesosternum. The position of the anterior articulating surfaces (character 3; Figs. 8C, D) has been subject to seven changes of state (Table 2), arising independently three times and reverting to the ancestral condition four times. I do not know how the anterior articulating surfaces function, so the significance of the repeated changes in state is unknown to me.

In Orthostethus (and possibly Probothrium), the effect of the "jump" may be simply to startle the bird. The mucro of Orthostethus is similar to Fig. 6D; the mesosternum is shown in Fig. 7E. Unlike other Elaterini, in which the margins of the fossa gradually slope up to the level of the mesocoxae (Figs. 7C, D, F-H), the abrupt slope of the fossal margins in Orthostethus appear more suited for trapping an object struck by the mucro. Species of Orthostethus are relatively large (up to 35mm in length). The effect of having the beak suddenly and violently pinched between the prosternal mucro and the margins of the mesosternal fossa could be quite startling. These modifications can be viewed as enhancing the effectiveness of the "jump" mechanism.

The modifications of the subpronotal lobe also involve parts of the "jump" mechanism. Preliminary dissections of Agriotes fucosus, which has a subpronotal lobe as in Fig. 4I, revealed that muscle M2b of Larsén (1966) is attached to the lateral arms of the subpronotal lobe. This muscle raises the anterior end of the prothorax, setting the prosternal mucro in position for the friction hold against the mesosternum (Larsén, 1966; Evans, 1972). The point of attachment of this muscle is various in other species. Larsén (1966) states M2b attaches to the intersegmental membrane in Corymbites aeneus (Linnaeus) (Denticollinae: Ctenicerini), while Evans (1972) shows M2b attaching to the underside of the pronotum in Athous haemorrhoidalis (Fabricius) (Denticollinae: Denticollini). I have not dissected specimens with the ancestral state of this character, but I assume muscle M2b attaches to the subpronotal lobe in these taxa as well. The significance of the difference in point of attachment of M2b is not clear to me. Perhaps the increased sclerotization and subsequent increase in size of the subpronotal lobe provides a more secure or stronger site of attachment than the intersegmental membrane or underside of the pronotum.

Guryeva (1969) proposed that the ancestral larval habitat of Elateridae is dead wood in various stages of decay. This is the known habitat of the relatively more primitive taxa of Elaterini (Elater, Parallelostethus, Orthostethus). The development of the apicolateral groove

and enlarged terebral tooth of the right mandible could function to provide an enhanced shearing surface between the left and right mandibles. An enhanced shearing surface suggests predatory behaviour, but this configuration is present in taxa with hypognathus mouthparts and thus are not assumed to be predatory. I have collected elaterids with prognathous mouthparts engaging in predatory behaviour, but have not observed those with hypognathous mouthparts doing so. On the mandibles of Elaterini I have examined, I have not seen scratches or wear patterns that would suggest repeated use. All taxa with a relatively large terebral tooth (descendents of Ancestor I; character 17) also have a distinct apicolateral groove (character 8, Table 2). The known habitat-in-common of larvae in the descendents of Ancestor I is soil (though species also occur in leaf litter and decayed wood). This suggests a possible significance of the enlarged terebral tooth and apicolateral groove. Larvae pupate in the larval habitat and adults must escape from there. Larvae of some species are known to form pupal cells at depths of up to 20cm below the soil surface (Hawkins, 1936, for Agriotes mancus; Lafrance & Cartier, 1964, for Dalopius pallidus). Adults of the descendents of Ancestor I rarely exceed 15mm in length and lack obvious adaptations for digging. It seems to me that for these species, escaping the larval habitat presents a significant problem. In addition to the soil itself, roots of plants could present formidable additional obstacles. I propose that the mandibles are used to loosen and remove soil particles and shear plant roots enabling the adult to reach the soil surface. Abrasion by the frontal carina/supraantennal crests may also aid in loosening soil particles.

The modifications of the epipharngeal bar sclerites, female genitalia and gena do not appear to infringe on the evolutionary constraints imposed above. The epipharyngeal bar sclerites appear to support the epipharynx and may be sites of muscle attachment. The functional significance of the increase in size in unclear.

Shifting the origin of the spermathecal duct closer to the posterior end of the bursa copulatrix makes the bursa more compact. This is correlated with a decrease in body size. Roughly linear bursae (Fig. 11A) are found in relatively larger species and recurved bursae (Fig. 11E) are found in relatively smaller species. Species in which the bursa has become secondarily linear (e.g., Glyphonyx; Fig. 11G) are among the smallest of the Elaterini studied. Increasing compaction of the bursa appears to have been accompanied by an increasing concentration of the bursal armature, as separate spines formed discrete fans and then spiny plates; armature was eventually eliminated in some

taxa (Adrastus, Sparsus group of Agriotes). The concentration and reduction of the bursal armature could also be an adjustment for smaller body size.

Several modifications of the ovipositor are discussed under 'Structural Features of Elaterini', but the polarity of the character states is uncertain. The sclerotized lateral margins of the baculi, enlarged and more heavily sclerotized tergum X, and the complete sclerotization of the gonocoxites coupled with the loss of a ventral suture and apical and lateral setae, appear to be modifications of the ovipositor which function to strengthen it and possibly remove structures that could be broken off. This probably enables eggs to be deposited in more solid substrates such as wood in various stages of decay. Guryeva (1969) proposed that rotting wood was the ancestral habitat for elaterids. The known larval habitat of species of Elater, Orthostethus, Parallelostethus and Probothrium is decaying wood; these four genera are among those with strengthened ovipositors. However, the larvae of Sericus (Sericosomini) are found in sand or sandy gravel, and humus-mixed soil under mosses and lichens (Palm, 1972). Sericus has a strengthened ovipositor, while other taxa in this kind of habitat do not (e.g., Agriotella). The presence of these character states in Sericus and relatively more primitive members of the Elaterini suggests a strengthened ovipositor is an ancestral character for the Elaterini + Sericosomini. However, both strengthened and unstrengthened ovipositors are found elsewhere in the Elaterinae and Elateridae and both states occur in the Sericosomini (Chiagosnius and Dolerosomus have unstrengthened ovipositors). A strengthened ovipositor probably has been lost and/or gained repeatedly in the evolution of the Elateridae.

The prolongation of the gena (Fig. 1C) could serve to protect the ventral surface of the head, but from what kind of threat is unclear.

The function and functional significance of the remainder of the character states is unclear to me, and further speculation is deferred until more information on the habitat and way of life of these beetles can be obtained.

Biogeographical Considerations

Discussion of the zoogeographical history of the Elaterini must, out of necessity, be brief and only in general terms. Except for the trivial example of monobasic genera, Ctenoplus is the only genus for which I have examined most of the described species. Thus, Ctenoplus is the only genus for which I can feel confident of monophyly as diagnosed. Most genera, as discussed above in the treatment of genera, I have reason to believe are not monophyletic. Lack of monophyly and inadequate information about distribution of terminal taxa renders detailed discussion of zoogeography futile.

I can see little evidence that the Elaterini had a Gondwanian origin. Taxa with such an origin typically have relatively primitive subtaxa restricted to temperate South America, Madagascar and/or temperate southern Africa, and Australia and/or New Zealand (Briggs, 1987). Panspoeus, described from New Zealand, is the only member of the Elaterini which fits this pattern. Although a member of the relatively more primitive Elater group, its systematic position within the group is unknown. Unlike other genera of the Elater group, the bursa copulatrix of Panspoeus bears discrete spiny plates, a derived character state within the Elaterini. Further collecting in temperate South America may show that Panspoeus also lives there. Although the genus was described from specimens collected in New Zealand, it has no obvious relatives in the Australasian region and the possibility that Panspoeus was introduced to New Zealand should be considered. If Panspoeus is found in South America, it may belong to the Neotropical radiation of Elaterini discussed below.

Since both the outgroup of the Elaterini and the relatively more primitive genera of Elaterini live in the northern hemisphere, I believe the Elaterini originated in Laurasia. Lack of fossils that can be assigned to the Elaterini and the uncertain position of the Elaterini within the Elateridae make it difficult to infer the time of appearance of the tribe. Relatively derived taxa of Elaterini appear in the fossil record by the Eocene (see below), so a mid- to late Cretaceous origin for the Elaterini may be probable.

Perhaps the most intriguing aspect of the biogeographical history of the Elaterini is the evolution of the genera I believe to be of Neotropical origin (the descendents of Ancestor H). The absence of relatively more primitive genera of the Elater group in South America suggests that a relatively more derived ancestor (Ancestor H) dispersed into South America. This event may have

occurred in the late Cretaceous via present day Central America. Biogeographer's maps in Briggs (1987, Map 5; reproduced here as Fig. 20) show a continuous land mass in present day Central America separated from present day western North America by a relatively narrow sea channel. I believe the ancestor of the Pomachilius, Agriotes and Adrastus groups originated in South America because of the evolution of three characters that are unique in the Elateridae. The distinctive fan-shaped clusters of spines on the bursa copulatrix (character 20, state 1; Fig. 11E) first appear in Ancestor I (Fig. 12), among relatively more derived genera of the Elater group restricted to the Neotropical region. The deeply notched anterior subpronotal lobe (character 21; Fig. 4I) first appears in Ancestor J (Fig. 12), also among relatively more derived genera of the Elater group restricted to the Neotropical region. Finally, the distinctively crenellated margin of the mesosternal fossa (character 24; Fig. 7D) first appears in Mesembria, a relatively more primitive genus of the Pomachilius group restricted to the Neotropical region.

At some point prior to the Eocene, the ancestor of the Agriotes and Adrastus groups (either Ancestors N and R in Fig. 12, or Ancestor MC in Fig. 15) dispersed out of South America. This event probably occurred in the Paleocene via the same route used by Ancestor H above. Biogeographer's maps in Briggs (1987, Map 6; reproduced here as Fig. 21) show a series of large islands in present day Central America separated from each other and North America by relatively narrow seas. By Eocene-Oligocene time, Adrastus, Glyphonyx, Silesis and Agriotes had evolved, since these genera have been identified in Baltic amber (Larsson, 1978). By the Miocene, Agriotes (Ectinus) (Becker, 1963) and what are now Old World species of Glyphonyx (Becker, 1963; Zaragosa Caballero, 1990), the relatively more primitive elements of Agriotes and Glyphonyx, were living in present day southern Mexico and Greater Antilles of the West Indies (Dominican amber). Both genera are represented in Chiapan amber (Becker, 1963; Zaragosa Caballero, 1990). Sometime after the Miocene, what are now New World species of Glyphonyx evolved, replacing the species of Glyphonyx represented in Chiapan and Dominican amber; see discussion of lobed tarsomeres (characters 28, 29) above.

In my opinion, the northern hemisphere representatives of the Pomachilius group (Dalopius, Agriotella, Betarmon and possibly the Criddlei group of Agriotes) are the result of one or more relatively recent invasions, probably dating from Pliocene time when the Isthmus of Panama became a continuous land connection between North and South America (Briggs, 1987). Three of the above four taxa appear to be

either closely related to or congeneric with a South American genus. I am unable to distinguish Agriotella from Cosmesus; Dalopius appears to have undescribed congeners in Brazil; and Betarmon is closely related to Pomachilius. As argued above, I believe the Pomachilius group originated in South America.

Further biogeographic analysis must await establishment of monophyletic groups in the genera of Elaterini.

CONCLUDING REMARKS

Much work remains to be done on the classification of the Elaterini, especially resolving the polychotomies in the reconstructed phylogeny. However, I do not believe it is possible, or advisable, to proceed further until the monophyly of the terminal taxa can be established. This is true particularly of the Elater group of genera and the Neotropical genera of the Pomachilius group. I intend to pursue this lengthy and undoubtably frustrating task.

A comment should be made on the potential value of elaterid larvae. I am convinced larvae will provide valuable insights into the classification of the Elaterini (and Elateridae in general), but unfortunately, knowledge of the structural features of elaterid larvae is no better than that of adults: most authors continue to place emphasis on character states that can be observed with little effort, and taxonomic conclusions are based on examination of few species in each genus. Admittedly, this is in part a limitation of the available data. Elaterid larvae are difficult and time-consuming to rear. To date, few larvae have been associated with their conspecific adults, and the majority of these are species from Europe and North America. My attempts at rearing larvae have not been stunningly successful, but I continue to try.

Finally, would I recommend studying elaterids to someone looking for a project? I would, but only if that person can honestly tell themselves that elaterids are simply the most wonderful creatures on this planet! The frustration of elaterid classification is so great that any study of elaterid systematics must be a labour of love.

LITERATURE CITED

Acorn, J.H. and G.E. Ball, 1991. The mandibles of some adult ground beetles: structure, function and the evolution of herbivory (Coleoptera: Carabidae). Canadian Journal of Zoology, 69:638-650.

Agajev, 1985. 'A new click-beetle genus'. Vestnik Zoologhii 5:66-67. [in Russian; from Zoological Record]

Arnett, R.H., Jr., 1955. Supplement and corrections to J.A. Hyslop's Genotypes of the Elaterid Beetles of the World. Proceedings of the United States National Museum, 103:599-619.

Arnett, R.H., Jr., 1962. Beetles of the United States, Fasc. 46, Elateridae, pp. 497-512. Catholic University of America Press, Washington.

Ax, P., 1987. The Phylogenetic System: The Systematization of Living Organisms on the Basis of their Phylogenesis. John Wiley & Sons, Chichester, 340 pp.

Baba, K. and H. Ohira, 1956. Some Elateridae from Sado, Tobi and Awa Is. (Honshu, Japan). Kontyû, 24:8-18.

Becker, E.C., 1956. Revision of the Nearctic species of Agriotes (Coleoptera: Elateridae). Canadian Entomologist, 88, supplement 1. 101 pp.

Becker, E.C., 1958. The phyletic significance of the female internal organs of reproduction in the Elateridae. Proceedings of the Tenth International Congress of Entomology, 1:199-205.

Becker, E.C., 1963. Three new fossil elaterids from the amber of Chiapas, México, including a new genus (Coleoptera). Journal of Paleontology, 37:125-128.

Becker, E.C., 1971. Five new species of Megapenthes from the southwestern United States, with a key to the Nearctic species (Coleoptera: Elateridae). Canadian Entomologist, 103:145-167.

Becker, E.C., 1972. A new species of Anchastus from Arizona and Baja California (Coleoptera: Elateridae). Coleopterists Bulletin, 26:121-123.

Becker, E.C., 1979. Notes on some New World and Palearctic species formerly in Athous Eschscholtz and Harminius Fairmaire with new synonymies (Coleoptera:

Elateridae). Canadian Entomologist, 111:401-415.

Berthold, A.A., 1827. Latreille's Naturliche Familien des Theirreichs. Aus dem Französischen. Mit Anmerkungen und Zusätzen. Weimar, 606 pp. [from Blackwelder, 1944]

Binaghi, G., 1940. Idiotarmon genere nuovo per Betarmon quadrivittatus Ragusa (Col. Elateridae). Bollettino della Società Entomologica Italiana, 72:99-102.

Blackwelder, R.E., 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, Parts 1-6. Smithsonian Institution, United States National Museum, Bulletin 185. 1492 pp.

Borg-Karlson, A.-K., L. Ägren, J. Dobson and G. Bergström, 1988. Identification and electroantennographic activity of sex-specific geranyl esters in an abdominal gland of female Agriotes obscurus (L.) and A. lineatus (L.) (Coleoptera, Elateridae). Experientia, 44:531-534.

Briggs, J.C., 1987. Biogeography and Plate Tectonics. (Developments in Palaeontology and Stratigraphy, 10). Elsevier, Amsterdam. 204 pp.

Brown, E.A. and A.J. Keaster, 1978. Internal reproductive glands as taxonomic characters in males of two species of Elateridae (Coleoptera). Canadian Entomologist, 110:108- 110.

Brown, W.J., 1933. Studies in the Elateridae II. Canadian Entomologist, 65:173-182.

Brown, W.J., 1934. The American species of Dalopius Esch. (Elateridae, Coleop.). Canadian Entomologist, 66:30-39, 66-72, 87-96, 102-110.

Burmeister, H.C.C., 1875. Nachschrift zu den Elaterina Argentina. Stettiner Entomologische Zeitung, 36:271-272. [from Blackwelder, 1944]

Calder, A.A., 1976. The New Zealand genus Metablax (Coleoptera: Elateridae) and its relationship to the Campsosterninae. New Zealand Journal of Zoology, 3:313-325.

Calder, A.A., 1978. The Neotropical genus Anaissus (Elateridae) and its relationship to the Pyrophorinae. Systematic Entomology, 3:295-306.

Calder, A.A., 1981. The Madagascan click-beetle genus Crepicardus (Elateridae) and its relationship to the Pyrophorinae. Systematic Entomology, 6:355-372.

Calder, A.A., 1986. Classification, relationships and distribution of the Crepidomeninae (Coleoptera: Elateridae). Australian Journal of Zoology, Supplementary Series No. 122, 222 pp.

Candèze, E.C.A., 1859. Monographie des Élatérides, tome deuxième. Mémoires de la Société royale des Sciences, Liége, vol. 14, pp. 1-543.

Candèze, E.C.A., 1860. Monographie des Élatérides, tome troisieme. Mémoires de la Société royale des Sciences, Liége, vol. 17, pp. 1-512.

Candèze, E.C.A., 1863. Monographie des Élatérides, tome quatrieme. Mémoires de la Société royale des Sciences, Liége, vol. 17, pp. 1-534.

Candèze, E.C.A., 1865. Élatérides nouveaux. Mémoires courannes, Academie royale des Sciences de Belgique, 17(1864):1-63.

Candèze, E.C.A., 1878. Élatérides nouveaux. Deuxième fascicule. Comptes-rendus de la Société entomologique de Belgique, 21:51-61, 75-85, 135-143, 161-172, 189-199 (separate pages 1-54).

Candèze, E.C.A., 1881. Élatérides nouveaux. Troisième fascicule. Mémoires de la Société royales des Sciences de Liége, 9:1- 117.

Candèze, E.C.A., 1887. Description d'Élatérides nouveaux, provenant de Normantown: Baie de Carpentaria (Australia septentrionale). Notes from the Leyden Museum, 9:285-290.

Candèze, E.C.A., 1889. Élatérides nouveaux. Quatrième fascicule. Annales de la Société entomologique de Belgique, 33:67-123 (separate pages 1-57).

Candèze, E.C.A., 1891. Catalogue méthodique des Élatérides connus en 1890. Liège. 246 pp.

Candèze, E.C.A., 1895a. Élatérides nouveaux. Cinquieme fascicule. Mémoires de la Société royales des Sciences de Liége, 18:1-77.

Candèze, E.C.A., 1895b. Mission scientifique de M. Ch. Alluaud dans le territoire de Diégo-Suarez (Avril-Août

1893). Les Élatérides de Madagascar. Annales de la Société entomologique de Belgique, 39:50-69.

Candèze, E.C.A., 1897. Élatérides nouveaux. Sixième fascicule. Mémoires de la Société royales des Sciences de Liége, 29:1-88.

Casari-Chen, S.A., 1984. Sistemático e evolução dos Hemirhipini Neotropicais (Pyrophorinae, Elateridae, Coleoptera). Revista Brasileira de Entomologia, 29:383-423.

Castelnau, F.L. de Laporte, Comte de, 1840. Histoire naturelle des insectes. Coléoptères. 1. cxxv + 135 pp. Paris [from Hayek, 1973]

Champlain, A.B. and J.N. Knull, 1932. Fermenting baits for trapping Elateridae and Cerambycidae (Coleop.). Entomological News, 43:253-257.

Champion, G.C., 1894-1896. Elateridae, in Godman, F.D. and O. Salvin, eds., Biologia Centrali-Americana, Insecta, Coleoptera, Vol. 3, part 1, pp. 258-584.

Cheshire, J.M. and D.C. Jones, 1988. Identification of the larva of Glyphonyx bimarginatus Schaeffer (Coleoptera: Elateridae). Journal of Entomological Science, 23:293-296.

Costa, C., 1990. Larva and pupa of Thoramus laevithorax (White, 1846) and the systematic position of the genus Thoramus Sharp, 1877 (Coleoptera, Elateridae, Pyrophorinae). Revista Brasileira de Entomologia, 36:223-227.

Costa, C. and S.A. Casari-Chen, 1984. Larvae of Neotropical Coleoptera. VIII. Elateridae: Agrypninae, Elaterinae and Physorhininae. Revista Brasileira de Entomologia, 28:315-328.

Dejean, P.F.M.A., 1829. Spécies général des coléoptères de la collection de M. le comte Dejean, vol.4. 520 pp. Paris. [from Blackwelder, 1944]

Dejean, P.F.M.A., 1833. Catalogue des coléoptères de la collections de M. le comte Dejean, livr. 1, pp. 1-96; livr. 2, pp. 97-176. Paris. [from Blackwelder, 1944]

Desbrochers des Loges, J., 1875. Opuscules entomologiques (Coléoptères). 56 pp. Gannat [from Hayek, 1973]

Dietrich, H., 1945. The Elateridae of New York State.

Cornell University Agricultural Experiment Station, Memoir 269. 79 pp.

Doane, J.F., J. Klinger and H.E. Welch, 1972. Parasitism of Agriotes obscurus Linnaeus (Coleoptera: Elateridae) by Hexamermis sp. (Nematoda: Mermithidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 45:299-300.

Dolin, V.G., 1975. 'Wing venation of click-beetles (Coleoptera, Elateridae) and its importance for taxonomy of the family.' Zoologicheskii Zhurnal, 54:1618-1633. [in Russian]

Dolin, V.G., 1978. 'Guide to the larvae of Click Beetles in the USSR'. Kiev, Urozhai, 124 pp. [in Russian]

Erichson, W.F., 1842. Berich über die Leistungen in der Naturgeschichte die Insecten, Arachniden, Crustaceen un Entomostraceen während des Jahres 1841. Archiv fur Naturgeschischte 8:83-287. [from Blackwelder, 1944]

Erichson, W.F., 1843. Archiv für Naturgeschichte, 9:149-288 [from Neboiss, 1956]

Eschscholtz, J.F., 1829. Elaterites Eintheilung derselben in Gattungen. Entomologisches Archiv, 2:31-35 [from Becker, 1956]

Evans, M.E.G., 1972. The jump of the click beetle (Coleoptera, Elateridae) - a preliminary study. Journal of Zoology, 167:319-336.

Farris, J.S., 1988. HENNIG86 Reference, Version 1.5. Privately printed.

Fleutiaux, E., 1903. Contributions à la faune Indo-Chinoise. 18e Mémoire. Deuxiéme addition aux Cicindelidae et Elateridae. Annales de la Société entomologique de France, 71:569-580.

Fleutiaux, E., 1906. Élatérides nouveaux de Madagascar [Col.]. Bulletin de la Société entomologique de France, 1906:199-200.

Fleutiaux, E., 1907. Revision des Elateridae du Chili. Revista Chilena de Historia Natural, 11:160-232.

Fleutiaux, E., 1931a. Contributions à la faune de l'Indochine française. Bulletin de la Société entomologique de France, 1931:73-75.

Fleutiaux, E., 1931b. Note sur un genre nouveau d' Elateridae. Bulletin de la Société entomologique de France, 1931:20-30.

Fleutiaux, E., 1932. Coléoptères des Iles mascareignes. Mission scientifique de P. Carie (1910-1913). Melasidae et Elateridae. Annales de la Société entomologique de France, 101:25-39.

Fleutiaux, E., 1936. Les Élatérides de l'Indochine française, (sixième partie). Annales de la Société entomologique de France, 105:279-300.

Fleutiaux, E., 1939. Les Élatérides de l'Indochine française, septieme partie. Annales de la Société entomologique de France, 108:121-148.

Fleutiaux, E., 1940a. Élatérides nouveaux de l'Indochine française. Bulletin de la Société zoologique de France, 65:184-198.

Fleutiaux, E., 1940b. Élatérides nouveaux. Bulletin et Annales de la Société entomologique de Belgique, 80:89-104.

Fleutiaux, E., 1940c. Les Élatérides de l'Indo-chine française. Huitième et dernière partie. XVIII. Subfamily Adrastinae. Annales des la Société entomologique de France, 109:19-40.

Fleutiaux, E., 1941. Tableau des genres et sous-genres des Octocryptitae et des Agrypnitae. Revue française d'Entomologie, 8:42-48.

Fleutiaux, E., 1947. Révision des Élatérides (Coléoptères) de l'Indochine française. Musée Heude. Notes d'Entomologie Chinoise XI, Fasc. 8, 233-420.

Frost, S.W. and H. Dietrich, 1929. Coleoptera taken from bait-traps. Annals of the Entomological Society of America, 22:427-437.

Glen, R., 1944. Contributions to a knowledge of the larval Elateridae (Coleoptera): No. 3; Agriotes Esch. and Dalopius Esch. Canadian Entomologist, 76:73-87.

Gullan, P.J., 1977. A revision of the genus Anilicus Candèze, with notes on related genera (Coleoptera: Elateridae). Memoirs of the National Museum of Victoria, 38:209-230.

Guryeva, Ye. L., 1969. Some trends in the evolution of

click beetles (Coleoptera, Elateridae). Entomological Review, 48:154-159.

Guryeva, Ye. L., 1971. A review of the wireworm species of the genus Dalopius Esch. (Coleoptera, Elateridae) in the fauna of the USSR. Entomological Review, 50:502-506.

Guryeva, Ye. L., 1972. A review of Palearctic species of the genus Agriotes Esch. (Coleoptera, Elateridae). Entomological Review, 51:509-520.

Guryeva, Ye. L., 1974. Thoracic structure of click beetles (Coleoptera, Elateridae) and the significance of the structural characters for the system of the family. Entomological Review, 53:67-79.

Guryeva, Ye. L., 1976. New click beetles of the genus Adrastus Esch. (Coleoptera, Elateridae) from the Caucasus. Entomological Review, 55:65-68.

Guryeva, Ye. L., 1979a. Systematics and synonymy in the subfamily Elaterinae (Coleoptera, Elateridae). Entomological Review, 58:53-54.

Guryeva, Ye. L., 1979b. Fauna of USSR. Coleoptera, Vol.12, No. 3. Click-beetles (Elateridae). Subfamily Elaterinae. Tribes Megapenthini, Physorhinini, Ampedini, Elaterini, Pomachiliini. 'Nauka" Publishing House, Leningrad. 453 pp.

Guryeva, Ye. L., 1983. 'New species and genus of the click-beetles (Coleoptera, Elateridae) from Iran.' Vestnik Zoologhii 3:81-82. [from Hayek, 1990; in Russian]

Hawkins, J.H., 1936. The Wheat Wireworm, Agriotes mancus Say, with notes on some other injurious elaterids. Maine Agricultural Experiment Station, Bulletin 381. 146 pp., 13 plates.

Hayek, C.M.F. von, 1973. A reclassification of the subfamily Agrypninae (Coleoptera: Elateridae). Bulletin of the British Museum (Natural History), Entomology, Supplement 20:1-309.

Hayek, C,M.F. von, 1979. Additions and corrections to 'A reclassification of the subfamily Agrypninae (Coleoptera: Elateridae)'. Bulletin of the British Museum (Natural History), Entomology series, 38:183-261.

Hayek, C.M.F. von, 1990. A reclassification of the Melanotus group of genera (Coleoptera: Elateridae). Bulletin of the British Museum of Natural History (Entomology), 59:37-115.

Hennig, W., 1966. Phylogenetic Systemtics. University of Illinois Press, Urbana, Chicago, London. 268 pp.

Horn, G.H., 1884. A study of some genera of Elateridae. Transactions of the American Entomological Society, 12:33-52.

Hyslop, J.A., 1915. Wireworms attacking cereal and forage crops. United States Department of Agriculture, Bulletin 156. 34 pp.

Hyslop, J.A., 1921. Genotypes of the elaterid beetles of the world. Proceedings of the United States National Museum, 58:621-680.

Iablokoff, A.Kh., 1943. Éthologie de quelques Élatérides du Massif de Fontainebleau. Mémoires du Muséum National d'Histoire Naturelle (nouvelle série), 13, fasc. 3, 81-160.

International Trust for Zoological Nomenclature, 1985. International Code of Zoological Nomenclature, 3rd Edition. University of California Press, Berkeley and Los Angeles. 338 pp.

Jacquelin du Val, P.N.C., 1860. Manuel entomologique. Genera des coléoptères d'Europe ..., vol. III. Paris. pp. 1-464, 125-200 [from Blackwelder, 1944]

Jakobson, G.G., 1913. Zhuki Rossicae, fasc, 10, pp. 721-864, pls. lxxvi-lxxxiii. [from Blackwelder, 1944]

Jewett, H.H., 1946. Identification of some larval Elateridae found in Kentucky. Kentucky Agricultural Experiment Station, Bulletin 489. 40 pp.

Kamm, J.A., H.G. Davis and L.M. McDonough, 1983. Attractants for several genera and species of wireworms (Coleoptera: Elateridae). Coleopterists Bulletin, 37:16-18.

Kiesenwetter, E.A.H. von, 1858. Naturgeschichte der Insecten Deutschlands..., Abt. 1, Coleoptera, Band, Lief, 2, Bogen 12-14, pp. 193-384. [from Blackwelder, 1944]

Kiesenwetter, E.A.H. von, 1859. Beiträge zur käferfauna

Griechenlands. Berliner Entomologische Zeitschrift, 3:17-34. [from Guryeva, 1979b]

Kirby, W., 1837. Insects. Coleoptera, in Richardson, Fauna Boreali-Americana; or the zoology of the northern parts of British America ..., 249 pp. Norwich. [from Blackwelder, 1944]

Kirk, H.B., 1922. Biological notes on Elateridae and Melasidae (Col.). Entomological News, 33:236-240.

Kishii, T., 1966. Elateridae of Kyoto and its adjacent regions. Biol. Lab. Heian High School, Kyoto, 54 pp. (privately published)

Kishii, T., 1976. Some new forms of Elateridae in Japan (XI). Bulletin of the Heian High School, 20:47-56.

Kishii, T., 1984. The Elaterid-beetles of the tribe Agriotini from Japan (COLEOPTERA: Elateridae, Elaterinae). "The Elateridae of Japan, 1". Bulletin of the Heian High School, 28:11-77.

Kishii, T., 1985. Some new forms of Elateridae in Japan (XVII). Bulletin of the Heian High School, 29:1-30.

Kishii, T., 1987. A taxonomic study of the Japanese Elateridae (Coleoptera), with the keys to the subfamilies, tribes and genera. Kyoto, 289 pp. (privately published)

Knull, J.N., 1947. Two new Elateridae (Coleoptera). Entomological News, 58:90-92.

Knull, J.F., 1959. Two new species of Agriotes (Coleoptera: Elateridae). Ohio Journal of Science, 59:356-357.

Kring, J.B., 1959. Predation and survival of Limonius agonus Say (Coleoptera: Elateridae). Annals of the Entomological Society of America, 52:534-537.

Lacordaire, Th., 1857. Histoire Naturelle des Insectes. Genera des Coléoptères, ou exposé méthodogique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome Quatrième. Librairie encyclopédique de Roret, Paris. 579 pp.

Lafrance, J. and J.J. Cartier, 1964. Distribution of wireworm population [sic] (Coleoptera: Elateridae) in unfrozen and frozen organic soils of southwestern Quebec. Phytoprotection, 45:83-87.

Lane, M.C., 1948. Some generic corrections in the Elateridae. I. Proceedings of the Entomological Society of Washington, 50:179-182.

Lane, M.C., 1965. Eleven new species of Pacific Northwest Elateridae. Proceedings of the Entomological Society of Washington, 67:177-192.

Lane, M.C., 1971. Elateridae excluding Cardiophorinae. Pp. 6-34 in Hatch, M.W., ed., The Beetles of the Pacific Northwest, Part V. University of Washington Press, Seattle, 662 pp.

Larsén, O, 1966. On the morphology and function of the locomotor organs of the Gyrinidae and other Coleoptera. Opuscula Entomologica, supplement 30. 242 pp.

Larsson, S.G., 1978. Baltic Amber - a Palaeobiological Study. Entomograph vol. 1. Scandinavian Science Press, Klampenborg, Denmark, 192 pp.

Latreille, P.A., 1810. Considérations générales sur l'order naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposés en familles. Paris, 444 pp. [from Blackwelder, 1944]

Latreille, P.A., 1834. Distribution méthodique et naturalle des genres de diverses tribus d'insectes coléoptères, de la famille des serricornes. Annales de la Société entomologique de France, 3:113-170. [from Blackwelder, 1944]

Lawrence, J.F., 1987. Rhinorhipidae, a new beetle family from Australia, with comments on the phylogeny of the Elateriformia. Invertebrate Taxonomy, 2:1-53.

Lawrence, J.F. and E.B. Britton, 1991. Chapter 35, Coleoptera (Beetles), pp. 543-683, in CSIRO (Division of Entomology), The Insects of Australia. A textbook for students and research workers, 2nd Edition, Volume II. Cornell University Press, Ithaca, New York. 1137 pp.

Leach, W.E., 1815. [Articles on entomology], in Brewster, Edinburgh encyclopaedie, vol. 9. Edinburgh [from Blackwelder, 1944]

LeConte, J.L., 1853. Revision of the Elateridae of the United States. Transactions of the American Philosophical Society, ser. 2, 10:405-508.

LeConte, J.L., 1863. List of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections, No. 140, pp. 1-49.

Leech, H.B., 1944. Note on Dalopius tristis and D. insulanus (Coleoptera, Elateridae). Proceedings of the Entomological Society of British Columbia, 41:25.

Leseigneur, L., 1972. Coléoptères Elateridae de la faune de France continentale et de Corse. Bulletin mensuel de la Société Linnéenne de Lyon, 41 (supplement):1-381.

Linnaeus, C., 1758. Systema naturae per regna tria naturae secundum classes, ordines, genera species, cum characteribus, differentiis, synonymis, locis, ed. 10, vol. 1, 823 pp. Holmiae [from Blackwelder, 1944]

Maddison, W.P., M.J. Donoghue and D.R. Maddison, 1984. Outgroup analysis and parsimony. Systematic Zoology, 33:83-103.

Méquignon, A., 1930. Notes synonymiques sur les Elatérides (Col.), 4e note. Bulletin de la Société entomologique de France, 1930(4):91-96.

Montrouzier, X., 1860. Essai sur la faune entomologique de la Nouvelle-Calédonie (Balade) et des Iles des Pins, Art, Lifu, etc. Annales de la Société entomologique de France, ser.3, 8:229-308, 867-916.

Motschulsky, V., 1859. Coléoptères nouveaux de la Californie. Bulletin de la Société Impériale des Naturalistes de Moscou, 32:122-185, 357-410. [from Blackwelder, 1944]

Mulsant, E. and J.B. Godart, 1853. Description d'un coléoptère inédit constituant un nouveau genre parmi les élatérides. Opuscules Entomologiques, pt. 2:181-184.

Neboiss, A., 1956. A check list of Australian Elateridae (Coleoptera). Memoirs of the National Museum of Victoria, 22(2):1-75.

Neboiss, A., 1961. Additions and corrections to the checklist of Australian Elateridae. Memoirs of the National Museum of Victoria, 22(22):1-29.

Ohira, H, 1960. Studies on the morphology of the elaterid larvae of Japan (XIII). Kontyû, 28:27-33. [in

Japanese; from Kishii, 1987]

Ohira, H., 1962a. New or little-known Elateridae from Japan, III. (Coleoptera). Kontyû, 30:198-201.

Ohira, H., 1962b. New or little-known Elateridae from Japan, IV. Kontyû, 30:262-264.

Ohira, H., 1966. Notes on some Elateridae-beetles from Formosa II. Kontyû, 34:266-274.

Ohira, H., 1970. The Elateridae of the Ryukyu Archipelago, VIII (Coleoptera). Bulletin of the Aichi University of Education, 19(Natural Sciences):103-111. [from Kishii, 1987]

Ohira, H., 1971. Elateridae, supplement. Insects of Micronesia, 16(7):295-300.

Ohira, H., 1973a. Elaterid beetles from Borneo in the Bishop Museum (Coleoptera). Pacific Insects, 15:103-137.

Ohira, H., 1973b. Notes on some elaterid-beetles from Japan (XI). Kontyû, 41:99-101 [in Japanese, English summary]

Ohira, H., 1990. Notes on the Genus Silesis (Elateridae) from Japan. Entomological Review of Japan, 45:73-75.

Owen, J.A., A.A. Allen, I.S. Carter and C.M.F. von Hayek, 1985. Panspoeus guttatus Sharp (Col., Elateridae) new to Britian. Entomologist's Monthly Magazine, 121:91-95.

Palm, T., 1972. Die skandinavischen Elateriden-Larven (Coleoptera). Entomologica Scandinavica, Supplementum 2. 63 pp.

Pascoe, F.P., 1885. List of the Curculionidae of the Malay Peninsula. Annali Mus. civ. Stor. nat. Giacomo Doria, 22:201-331. [from Hayek, 1973]

Platia, G. and L. Bartolozzi, 1988. Contributo alla conoscenza degli Elateridi della Calabria (Coleoptera Elateridae). Redia, 71:61-97.

Platia, G. and M. Marini, 1990. Gli Elateridi (Coleoptera) della collezione Andrea Fiori, conservati nel Museo di Zoologia dell'Università di Bologna. Giornale italiano di Entomologia, 5:31-47.

Platia, G. and R. Schimmel, 1991a. Il genere Silesis Candèze nella regione indiana e cinese (Coleoptera, Elateridae, Adrastini). Fragmenta Entomologica, Roma, 23(1):101-177.

Platia, G. and R. Schimmel, 1991b. Descrizione di nuove specie di Elateridi di Grecia e Turchia con chiave per due gruppi di specie. Lavori - Società Veneziana di Scienze Naturali, 16:131-142.

Platia, G. and R. Schimmel, 1992. Descrizione di nuove specie di Elateridi di Grecia e Turchia (Coleoptera, Elateridae). Lavori - Società Veneziana di Scienze Naturali, 17:87-95.

Platia, G. and R. Schimmel, 1993a. Descrizione di nuove specie di Elateridi di Grecia e Turchia con note su alcuni Agriotes Eschscholtz (Coleoptera, Elateridae). Lavori - Società Veneziana di Scineze Naturali, 18:51-57.

Platia, G. & R. Schimmel, 1993b. Nuove specie e nuovi reperti di Silesis Candèze della regione indiana e cinese. Fragmenta Entomologica, Roma, 25(1):117-127.

Reiche, L. and F. de Saulcy, 1857. Espèces nouvelles ou peu connues de Coléoptères recueillies par M. F. de Saulcy dans son Voyage en Orient. Annales de la Société entomologique de France, 4:385-442. [from Hayek, 1973]

Reitter, E., 1911. Fauna Germanica. Die Käfer des Deutschen Reiches. Nach der analytischen Methode bearbeitet, vol. 3, 436 pp. Lutz, Stuttgart.

Roache, L.C., 1961. A revision of the North American elaterid beetles of the tribe Elaterini (Coleoptera: Elateridae). Transactions of the American Entomological Society, 86:275-324.

Roache, L.C., 1963. A revision of the genus Oxygonus LeConte with a description of one new species (Coleoptera: Elaterini) (Tribe: Agriotini). Coleopterists Bulletin, 17:101-108.

Rudolph, K., 1982. Beiträge zur Insektenfauna der DDR: Coleoptera - Elateridae. Faunistische Abhandlungen, 10:1-109.

Savely, H.E., 1939. Ecological relations of certain animals in dead pine and oak logs. Ecological Monographs, 9:321-385.

Schaeffer, C., 1916. New species of the family Elateridae (Col.). Journal of the New York Entomological Society, 24:256-267.

Schenkling, S., 1925. Pars 80. Elateridae, I, pp. 1-263, in Schenkling, S., ed., Coleopterorum catalogus auspiciis et auxilio W. Junk, Berlin and 's-Gravenhage.

Schenkling, S., 1927. Pars 88. Elateridae, II, pp. 265-636, in Schenkling, S., ed., Coleopterorum catalogus auspiciis et auxilio W. Junk, Berlin and 's-Gravenhage.

Schwarz, O., 1896. Neue Elateriden-Arten. Deutsche Entomologische Zeitschrift, 1896:97-104.

Schwarz, O., 1900a. Verzeichniss der von Hrn. Dr. Schultheiss in N.O.-Sumatra gesammelten Elateriden nebst Beschreibung einiger neuer Arten. Deutsche Entomologische Zeitschrift, 1900:89-97.

Schwarz, O., 1900b. Neue exotische Elateriden. Deutsche Entomologische Zeitschrift, 1900:305-358.

Schwarz, O., 1901. Aenderung des Gattungsnamens Pomachilioides m. in Paracosmesus m. Deustche Entomologische Zeitschrift, 1901:38.

Schwarz, O., 1902. Ueber die Elateriden-Gattungen Protelater Sharp und Anaspasis Cand. und ihre systematische Stellung nebst Beschreibung einer neuen Gattung und Art. Deutsche Entomologische Zeitschrift, 1902:364-366.

Schwarz, O., 1906-1907. Elateridae, in Wytsman, P., Genera Insectorum. Coleoptera, Fascicules 46A, 46B, 46C, 370 pp. Bruxelles.

Serville, J.G.A.-, 1834. Nouvelle classfication de la famille des longicornes (suite). Annales de la Société entomologique de France (ser.1), 3:5-110.

Sharp, D., 1877. On the Elateridae of New Zealand. Annals and Magazine of Natural History, 19:396-413.

Shpeley, D. and G.E. Ball, 1993. Classification, reconstructed phylogeny and geographical history of the New World species of Coptodera Dejean (Coleoptera: Carabidae: Lebiini). Proceedings of the Entomological Society of Ontario, 124:1-182.

Smith, J.W. and E.U. Balsbaugh, Jr., 1984. A taxonomic

revision of the Nearctic species of Glyphonyx (Coleoptera: Elateridae) with notes on G. quadraticollis Champion. North Dakota Insects, Shafer-Post Series, No. 16. 86 pp.

Solier, A.J.J., 1851. Orden III. Coleopteros, in Gay, Historia fisica y politica de Chile, Vol. 5, pp. 1-285 [from Blackwelder, 1944]

Stephens, J.F., 1830. Illustrations of British entomology; or a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata, vol. 3, pp. 1-374. London. [from Blackwelder, 1944]

Stibick, J.N.L., 1970. A revision of the genus Leptoschema of California with a key to related genera (Coleoptera: Elateridae). Pan-Pacific Entomologist, 46:153-166.

Stibick, J.N.L., 1971. The generic classification of the Negastriinae (Coleoptera: Elateridae). Pacific Insects, 13:371-390.

Stibick, J.N.L., 1979. Classification of the Elateridae (Coleoptera). Relationships and classification of the subfamilies and tribes. Pacific Insects, 20:145-186.

Tanner, V.M., 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society, 53:5-50.

Thomas, C.A., 1940. The biology and control of wireworms. Pennsylvania Agriculture Experiment Station, Bulletin 392. 90 pp.

Thomas, C.A., 1941. The Elateridae of Pennsylvania. Journal of the New York Entomological Society, 49:233-263.

Tschinkel, W.R. and J.T. Doyen, 1980. Comparative anatomy of the defensive glands, ovipositors and female genital tubes of tenebrionid beetles (Coleoptera). International Journal of Insect Morphology and Embryology, 9:321-368.

Watrous, L.E. and Q.D. Wheeler, 1981. The out-group comparison method of character analysis. Systematic Zoology, 30:1-11.

Westwood, J.O., 1838. Synopsis of the genera of British insects, signatures B-D, in An introduction to the modern classfication of insects; founded on the natural habits and corresponding organisation of the different families, volume 1, pp. 1-462. London [from Blackwelder, 1944]

Wiley, E.O., D. Siegel-Causey, D.R. Brooks and V.A. Funk, 1991. The Compleat Cladist. A Primer of Phylogenetic Procedures. University of Kansas Museum of Natural History, Special Publication No. 19. 158 pp.

Wilkinson, A.T., 1963. Wireworms of cultivated land in British Columbia. Proceedings of the Entomological Society of British Columbia, 60:3-17.

Zacharuk, R.Y., 1958a. Structures and functions of the reproductive systems of the Prairie Grain Wireworm, Ctenicera aeripennis destructor (Brown) (Coleoptera: Elateridae). Canadian Journal of Zoology, 36:725-751.

Zacharuk, R.Y., 1958b. Note on two forms of Hypolithus bicolor Esch. (Coleoptera: Elateridae). Canadian Entomologist, 90:567-568.

Zacharuk, R.Y., 1963. Comparative food preferences of soil-, sand-, and wood-inhabiting wireworms (Coleoptera, Elateridae). Bulletin of Entomological Research, 54:161-165.

Zaragoza Caballero, S., 1990. Descripción de una especie nueva fósil de Glyphonyx Candeze (Coleoptera: Elateridae, Adrastinae) del ámbar de Simojovel, Chiapas, México. Anales Inst. Biol. Univ. Nac. Autón. México, Ser. Zool., 61:147-151.

Table 1: Summary of possible affinities of taxa excluded from Elaterini and Sericosomini. See text for details.

GENUS	POSSIBLE PLACEMENT
Acroniopus Erichson	Denticollinae
Anaspasis Candèze	Oestodinae: Oestodini (Stibick, 1979)
Anilicoides Candèze	Denticollinae
Anilicopsis Schwarz	Pyrophorinae
Anilicus Candèze	Denticollinae
Ascesis Candèze	Denticollinae
Betarmonides Schwarz	Denticollinae
Campylomorphus Jacq. du Val	Denticollinae: Ctenicerini
Candanius Hayek	Pyrophorinae: Agrypnini (Hayek, 1979)
Cardiorhinus Eschscholtz	Denticollinae (Lawrence, 1987)
Compshelus Candèze	incertae sedis
Dicteniophorus Candèze	Denticollinae
Doloporus Candèze	incertae sedis
Heschatroxus Candèze	Denticollinae
Hypodesis Latreille	Denticollinae (Lawrence, 1987)

Idolus Desbrochers	Pyrophorinae: Conoderini
Ludigenus Candèze	Denticollinae: Ctenicerini?
Mecastrus Sharp	Elaterinae: Megapenthini or Ampedini
Monelasmus Candèze	Elaterinae: Physorhinini
Nycterilampus Montrouzier	Pyrophorinae
Ochosternus Candèze	Denticollinae
Oxygonus LeConte	Denticollinae: Ctenicerini
Paranilicus Candèze	Denticollinae
Paranius Champion	Elaterinae: Megapenthini
Pomachilioides Candèze	Elaterinae: Physorhinini
Protelater Sharp	Oestodinae: Oestodini (Stibick, 1979)
Psiloniscus Candèze	Elaterinae: Megapenthini?
Scelisus Candèze	Pyrophorinae: Agrypnini (Hayek, 1973)
Smiliceroides Schwarz	Elaterinae: Megapenthini
Somomecus Solier	Denticollinae: Ctenicerini?
Sphaenelater Schwarz	Oestodinae: Sphaenelaterini (Stibick, 1979)
Thoramus Sharp	Pyrophorinae (Costa, 1990)
Tomicephalus Latreille	Denticollinae

Table 2: Distribution of phylogenetically designated character states among taxa of the tribe Elaterini. See text for details of characters.

	CHARACTERS AND CHARACTER STATES																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
TAXON																	
Sericosomini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanobius	1	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0
Neotrichophorus (Old World)	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Pittonotus	1	1	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0
Diplostethus	1	1	1	0	1	0	1	1	1	0	1	1	1	1	0	0	0
Neotrichophorus (New World)	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0
Atractopterus	1	1	0	1	0	0	0	0	0	1	0	1	3	0	1	0	0
Leptoschema	1	1	1	?	0	0	?	0	0	0	0	?	3	0	0	?	0
Orthostethus	1	1	1	1	0	0	0	1	0	0	0	1	2	1	1	1	0
Elater	1	1	0	2	1	0	0	0	0	0	0	1	2	0	0	1	0
Parallelostethus	1	1	1	1	1	0	0	0	0	0	0	1	2	0	0	0	0
Probothrium	1	1	1	0	0	0	1	1	0	0	1	1	3	0	1	0	0
Agelasinus	1	1	0	0	0	0	1	1	0	0	0	0	3	0	0	0	1
Ypsilostethus	1	1	0	0	0	1	1	1	0	0	0	0	3	0	1	0	1
Mesembria	1	?	0	0	0	1	1	1	0	0	?	0	3	0	?	0	?
Dalopius	1	1	0	0	0	0	1	1	0	0	0	0	3	0	1	0	1
Agriotella/ Cosmesus	1	1	0	0	0	0	1	1	0	0	0	0	3	0	1	0	1
Deromecus	1	1	0	0	0	0	1	1	0	0	0	1	3	0	1	0	1
Agriotes (Ectinus)	1	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1
Agriotes (sensu stricto)	1	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	1
Medonia	1	?	0	0	0	0	1	1	0	0	?	0	4	0	?	0	?
Pseudoderomecus	1	1	1	0	0	1	1	1	0	0	0	0	3	0	0	0	1
Betarmon	1	1	0	0	0	0	1	1	0	0	0	0	3	0	1	0	1
Paracosmesus	1	1	0	0	0	0	1	1	0	0	0	0	3	0	1	0	1
Pomachilius	1	1	0	0	0	0	1	1	0	0	0	0	3	0	1	0	1
Adrastus	1	1	0	0	0	0	1	1	0	0	0	1	4	0	1	0	1
Synaptus	1	1	0	0	0	0	1	1	0	1	0	1	4	0	1	0	1
Parasilesis	1	1	0	0	0	0	1	1	0	0	0	1	4	0	1	0	1
Ctenoplus	1	1	0	0	0	1	1	1	0	1	0	0	4	0	1	0	1
Peripontius	1	1	0	0	0	0	1	1	0	0	0	0	4	0	1	0	1
Glyphonyx	1	1	0	0	0	0	1	1	0	0	0	0	4	0	1	0	1
Silesis	1	1	0	0	0	0	1	1	0	0	0	0	4	0	1	0	1

Table 2 (continued)

TAXON	CHARACTERS AND CHARACTER STATES													
	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Sericosomini	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphanobius	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotrichophorus (Old World)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pittonotus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplostethus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neotrichophorus (New World)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atractopterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptoschema	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Orthostethus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elater	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parallelostethus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Probothrium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agelasinus	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Ypsilostethus	1	0	1	1	1	1	0	0	1	0	0	0	0	0
Mesembria	?	1	1	?	1	1	1	0	0	0	0	0	?	?
Dalopius	1	1	1	1	0	1	1	1	0	0	0	0	0	0
Agriotella/ Cosmesus	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Deromecus	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Agriotes (Ectinus)	0	1	2	1	0	1	1	1	0	1	0	0	0	0
Agriotes (sensu stricto)	1	1	2	1	1	1	1	1	0	1	0	0	0	0
Medonia	?	1	1	?	0	2	1	1	1	1	1	0	?	?
Pseudoderomecus	1	1	1	1	0	0	1	1	1	0	1	0	0	0
Betarmon	1	1	1	1	1	1	1	1	1	1	0	1	0	0
Paracosmesus	1	1	1	1	1	2	1	1	1	1	0	1	0	0
Pomachilius	1	1	1	1	1	2	1	1	1	1	0	1	0	0
Adrastus	1	1	0	1	0	1	1	1	0	1	0	0	2	1
Synaptus	1	1	2	1	1	1	1	1	0	1	0	1	1	0
Parasilesis	1	1	2	1	1	2	1	1	0	1	1	0	2	1
Ctenoplus	1	1	2	1	1	2	1	1	0	1	0	0	2	1
Peripontius	1	1	2	1	1	2	1	1	0	1	1	0	2	0
Glyphonyx	1	1	2	1	1	2	1	1	1	1	1	0	2	1
Silesis	1	1	2	1	1	2	1	1	0	1	1	0	2	1

Table 2 (continued)

TAXON	CHARACTERS AND CHARACTER STATES 32	33	34	35	36	37
Sericosomini	0	0	0	0	0	0
Aphanobius	0	0	0	0	0	0
Neotrichophorus (Old World)	0	0	0	0	0	0
Pittonotus	0	0	0	0	0	0
Diplostethus	0	0	0	0	0	0
Neotrichophorus (New World)	0	0	0	0	0	0
Atractopterus	0	0	0	0	0	0
Leptoschema	0	0	0	0	0	0
Orthostethus	0	0	0	0	0	0
Elater	0	0	0	0	0	0
Parallelostethus	0	0	0	0	0	0
Probothrium	0	0	0	0	0	0
Agelasinus	0	0	0	0	0	0
Ypsilostethus	0	0	2	0	0	0
Mesembria	?	?	0	0	0	0
Dalopius	0	0	0	0	0	0
Agriotella/ Cosmesus	0	0	0	0	0	0
Deromecus	0	0	0	0	0	0
Agriotes (Ectinus)	0	0	0	0	0	0
Agriotes (sensu stricto)	0	1	0	0	0	0
Medonia	?	?	0	0	0	0
Pseudoderomecus	0	0	0	0	0	0
Betarmon	0	0	0	0	0	0
Paracosmesus	0	0	0	0	0	0
Pomachilius	0	0	0	0	0	0
Adrastus	1	1	1	0	0	0
Synaptus	1	0	1	2	1	0
Parasilesis	1	1	1	2	1	1
Ctenoplus	1	1	1	1	1	2
Peripontius	1	1	1	2	1	2
Glyphonyx	1	1	1	2	1	2
Silesis	1	1	1	2	1	2

Table 3: Summary of Character State Changes in Figs. 12-19

Character	Taxa in which Change of State Appears	Number of Changes of State
1	Ancestor A	1
2	Ancestor A	1
3	Ancestor A, Agriotes (Ectinus), Pseudoderomecus, reversals in Pittonotus, Atractopterus, Elater, Ancestor I	7
4	Ancestors A, N; reversals in Ancestors D, H, and Leptoschema	5
5	Ancestors B, G	2
6	Aphanobius, Old World Neotrichophorus, Ancestor K, Pseudoderomecus	4
7	Ancestors B, H	2
8	Two possibilities: Ancestor C, Orthostethus, Ancestor H; or, Ancestors C, H	2 or 3
9	Ancestor C	1
10	Ancestor C, Atractopterus, Synaptus; reversal in Diplostethus	4
11	Ancestor D, Probothrium	2
12	Ancestors D, F, R, and Deromecus; reversals in Ancestors I, U, Leptoschema	7
13	State 1: Ancestor E State 2: Three possibilites, Ancestor G and Orthostethus, or, Ancestor F, or Ancestor F and Orthostethus State 3: Two possibilites, Ancestor FB, or Ancestor FD and reversal in Orthostethus State 4: Medonia, Ancestor R	State 1: 1 State 2: 1 or 2 State 3: 1 or 2 State 4: 2
14	Ancestor E, Orthostethus	2

15	Three possibilities: Atractopterus, Orthostethus, Probothrium, Ancestor J; or, Orthostethus, Ancestor FC, reversal in Agelasinus, Ancestor O; or, Ancestor FF, reversal in Agelasinus, Ancestor O	3 or 4
16	Two possibilites: Pittonotus and Ancestor FA; or, Pittonotus, Orthostethus and Ancestor G	2 or 3
17	Ancestor I	1
18	Ancestor I, reversal in Agriotes (Ectinus)	2
19	Ancestor I, reversal in Ypsilostethus	2
20	State 1: Ancestor I State 2: Ancestors N, S	State 1: 1 State 2: 2
21	Ancestor J	1
22	Three possibilities: Ancestors K, M, reversals in Agriotes (Ectinus), Ancestor O, Adrastus; or, Ancestors K, MB, Agriotes (s. s.), Ancestor S; or Ancestors K, ME, Agriotes (s.s.), reversal in Adrastus	4 or 5
23	State 1: Ancestor J, reversal in Pseudoderomecus State 2: Medonia, Ancestors Q, T	State 1: 2 State 2: 3
24	Mesembria, Ancestor L	2
25	Ancestor L	1
26	Leptoschema, Ypsilostethus, Ancestor M/MA/MD; reversal in ancestors N, R	5
27	Ancestor M, reversal in Pseudoderomecus	2
28	Two possibilities: Ancestors O, T, reversal in Ctenoplus; or, Ancestors O, TB, Parasilesis	3
29	Ancestor P, Synaptus	2
30	State 1: Synaptus State 2: Adrastus, Ancestor T	State 1: 1 State 2: 2

31	Adrastus, Ancestor T	2
32	Ancestor R	1
33	Agriotes (s.s.), Adrastus, Ancestor T	3
34	Ancestor R	1
35	State 1: Ctenoplus State 2: ancestor S; reversal in Ctenoplus	State 1: 1 State 2: 2
36	Ancestor S	1
37	State 1: Ancestor T State 2: Ancestor U	State 1: 1 State 2: 1

Figure 1. Scanning electron micrographs of head structures. A-C, gena, lateral; A: Ampedus sp., B: Sericus incongruus, C: Dalopius marginatus. D-G, head, frontal; D: Deromecus vulgaris, E: Glyphonyx sp., F: Paracosmesus sp., G: Dalopius. H-J, periocular space, anterolateral; H: Adrastus sp., I: Synaptus filiformis, J: Ctenoplus brunneus. as - antennal socket, e - compound eye, fc - frontal carina, ge - gena, p - periocular pits, pg - periocular groove, su - supraantennal crests. Scale bar = 200 µm.

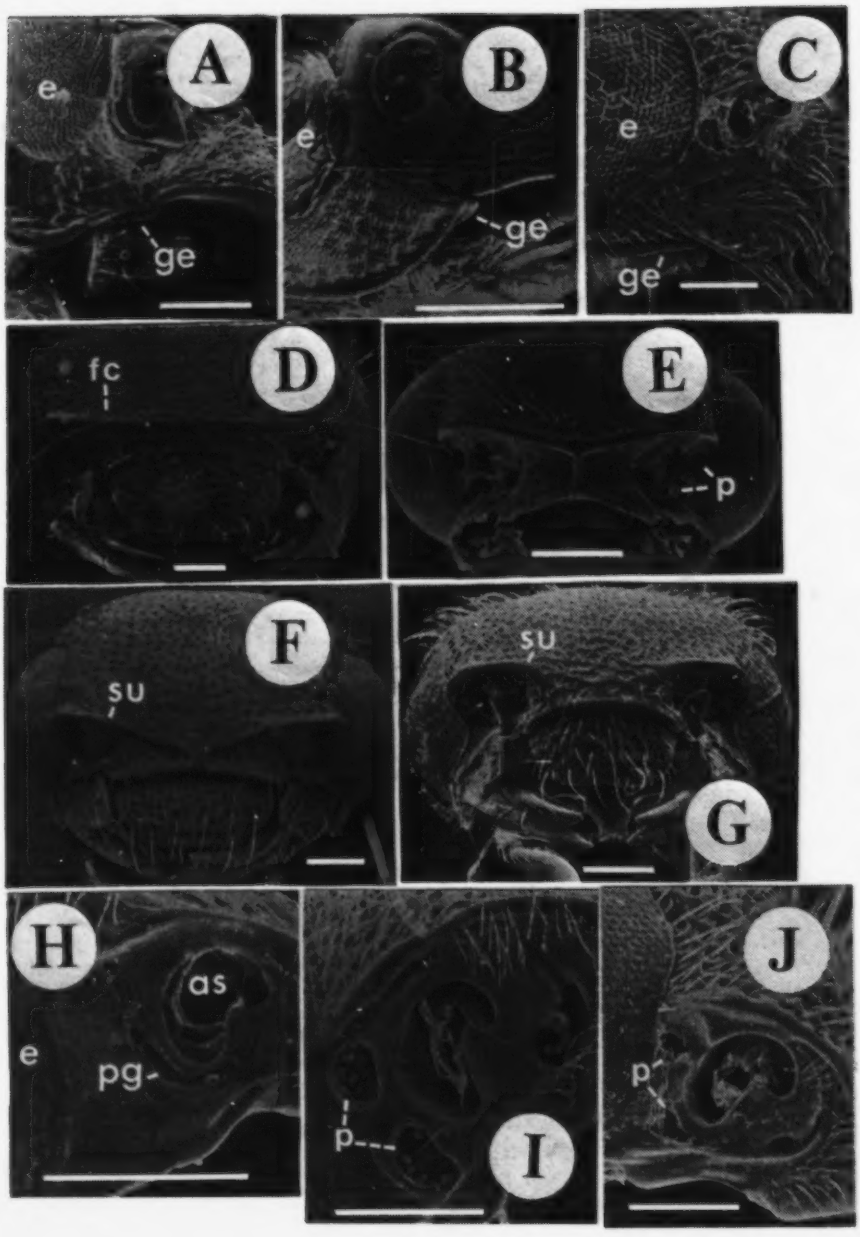
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Figure 2. Photographs of epipharynx. A: Elater ferrugineus; B: Neotrichophorus guillebeaui; C: Parallelostethus attenuatus; D: Agriotes (Ectinus) aterrimus; E: Neotrichophorus carolinensis; F: Pomachilius linearis; G: Adrastus sp. es - epipharyngeal bar sclerites. Scale bar = 0.25 mm.

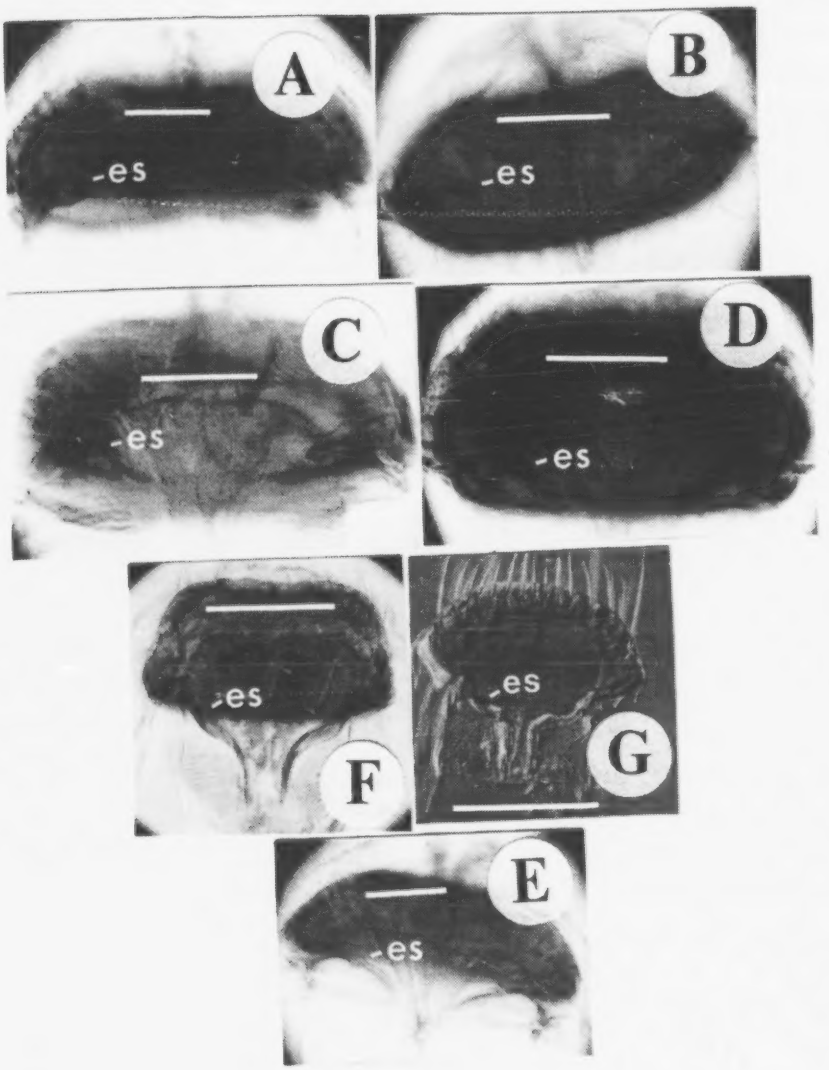
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Figure 3. Scanning electron micrographs of mandibles. A: Sericus incongruus, right mandible, lateral; B: Atractopterus honestus, right mandible, lateral; C: Neotrichophorus carolinensis, right mandible, occlusal; D: Dalopius marginatus, right mandible, occlusal; E: Atractopterus honestus, right mandible, dorsal; F, G, H: Synaptus filiformis, right mandible, dorsal, lateral, left mandible, lateral, respectively; I: Glyphonyx sp., right mandible, occlusal; J: Synaptus filiformis, right mandible, occlusal; K: Glyphonyx sp., right mandible, anterodorsal. b - basal face, be - basal expansion of mandible, d - dorsal mandibular condyle, mg - apicolateral groove of right mandible, om - membranous fringe, t - terebral tooth, v - ventral mandibular condyle. Scale bar = 200 μm.

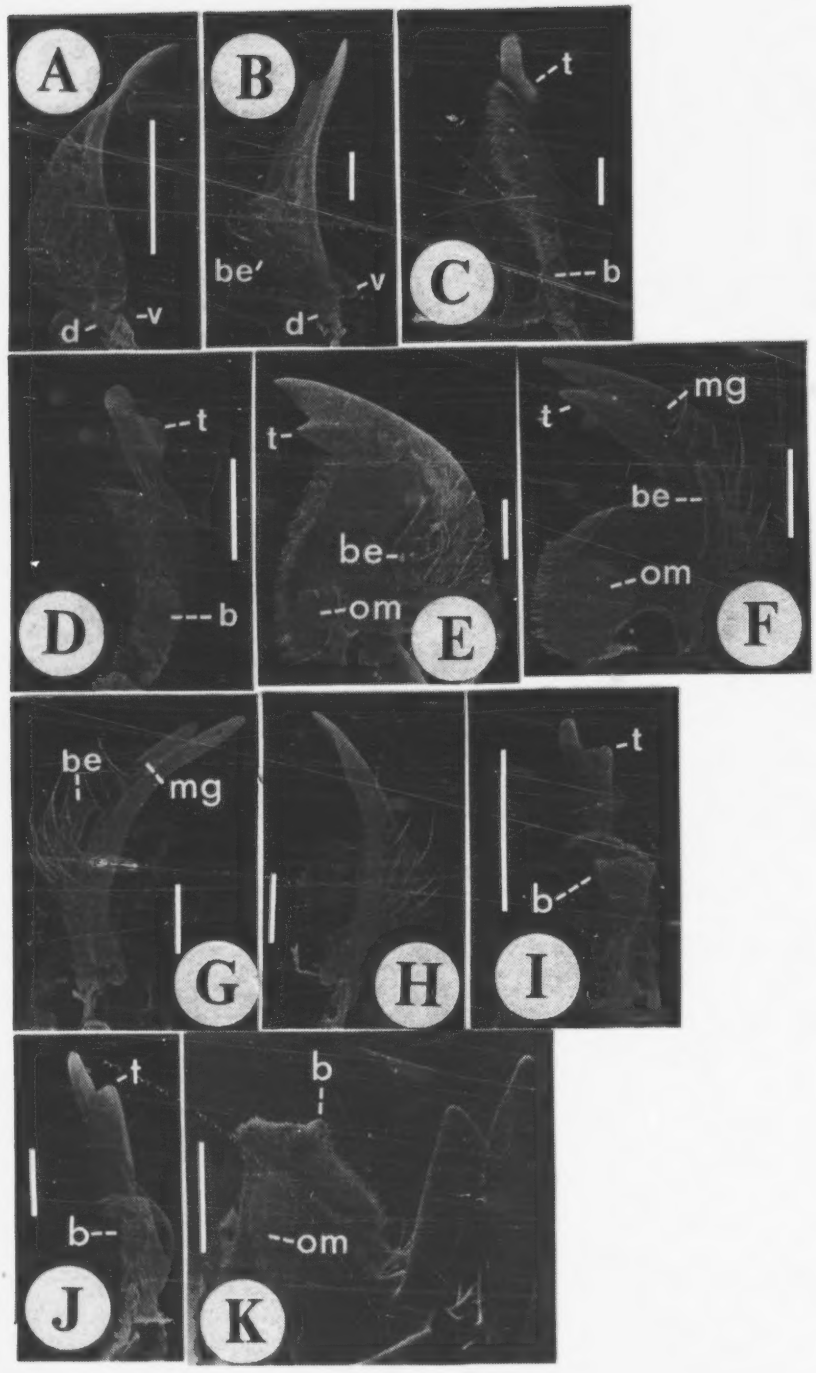
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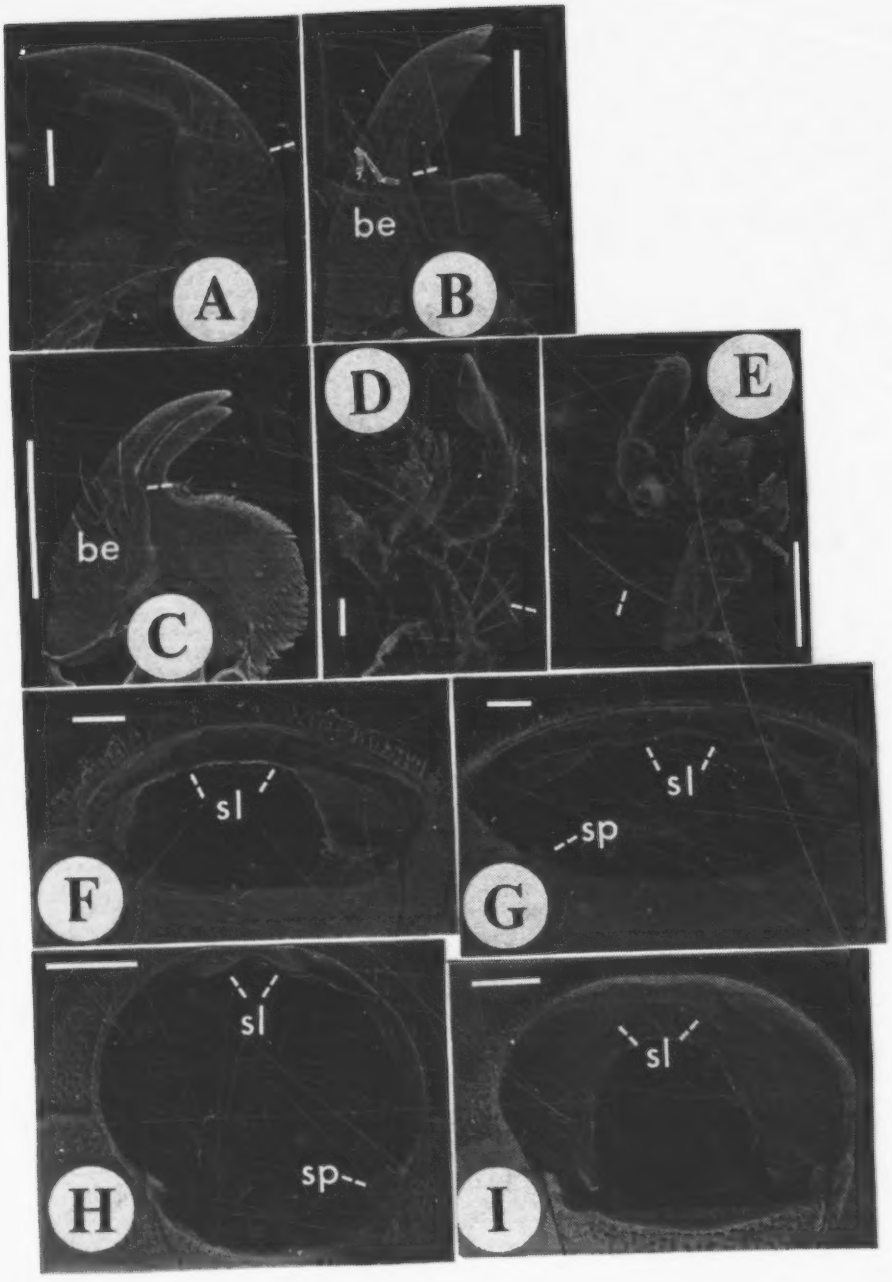
Figure 4. Scanning electron micrographs of mandibles, maxilla and pronota. A: Neotrichophorus carolinensis, right mandible, dorsal; B: Synaptus filiformis, left mandible, dorsal; C: Glyphonyx sp., left mandible, dorsal; D: Neotrichophorus carolinensis, maxilla, ventral; E: Dalopius marginatus maxilla, ventral; F: Atractopterus honestus, prothorax, anteroventral; G: Neotrichophorus carolinensis, prothorax, anteroventral; H: Diplostethus setosus, prothorax, anteroventral; I: Dalopius marginatus, prothorax, anteroventral. be - basal expansion of mandible, sl - subpronotal lobe; sp - anterolateral sternal projection. Scale bar, A-E, H,I = 200 μm, F,G = 400 μm.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sl
I

Figure 5. Scanning electron micrographs of prothorax. A, B: Agriotes sp., ventral, anterolateral corner; C, D: Dalopius marginatus, ventral, anterolateral corner; E: Diplostethus setosus, hypomeron ventrolateral; F: Agelasinus sp., hypomeron, ventrolateral; G: Diplostethus setosus, apex of hind angle, lateral. h - hypomeron, ha - hind angle of pronotum, hm - mesal margin of hypomeron, lm - lateral carina of pronotum, m - prosternal mucro, ps - pronotosternal sutures, s - prosternum, sp - anterolateral prosternal projection. Scale bar = 400 μm.

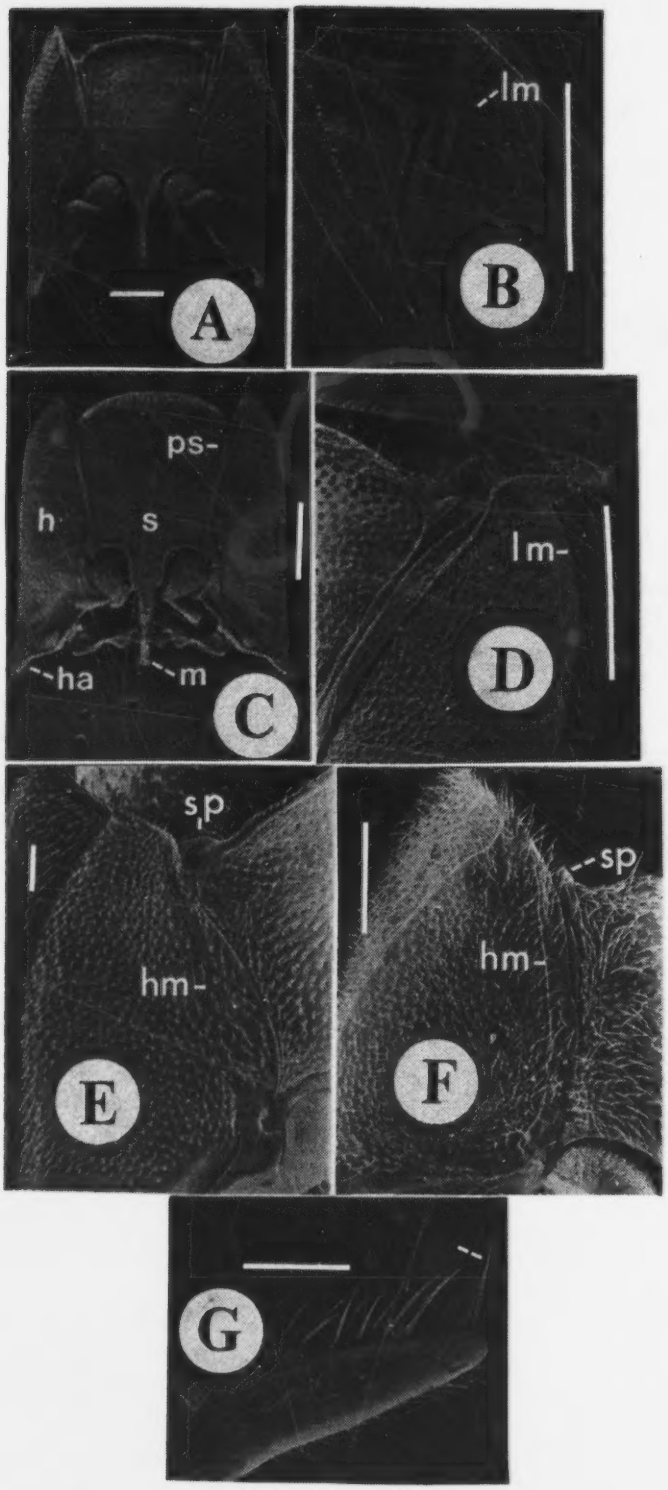

A
lm
B
ps-
h
s
ha
m
C
lm-
D
sp
hm-
E
sp
hm-
F
G

Figure 6. Scanning electron micrographs of prosternal mucro, A-E: lateral, ventral surface towards top of page, F-H: ventral, posterior towards top of page. A: Aphanobius sp.; B: Neotrichophorus carolinensis; C: Diplostethus setosus; D: Pittonotus theseus; E: Agelasinus sp.; F: Parasilesis musculus; G: Silesis grisescens; H: Peripontius terminalis. ds - dorsal surface of prosternal mucro, vs - ventral surface of prosternal mucro, vt - ventral tooth of prosternal mucro. Scale bar = 400 µm.

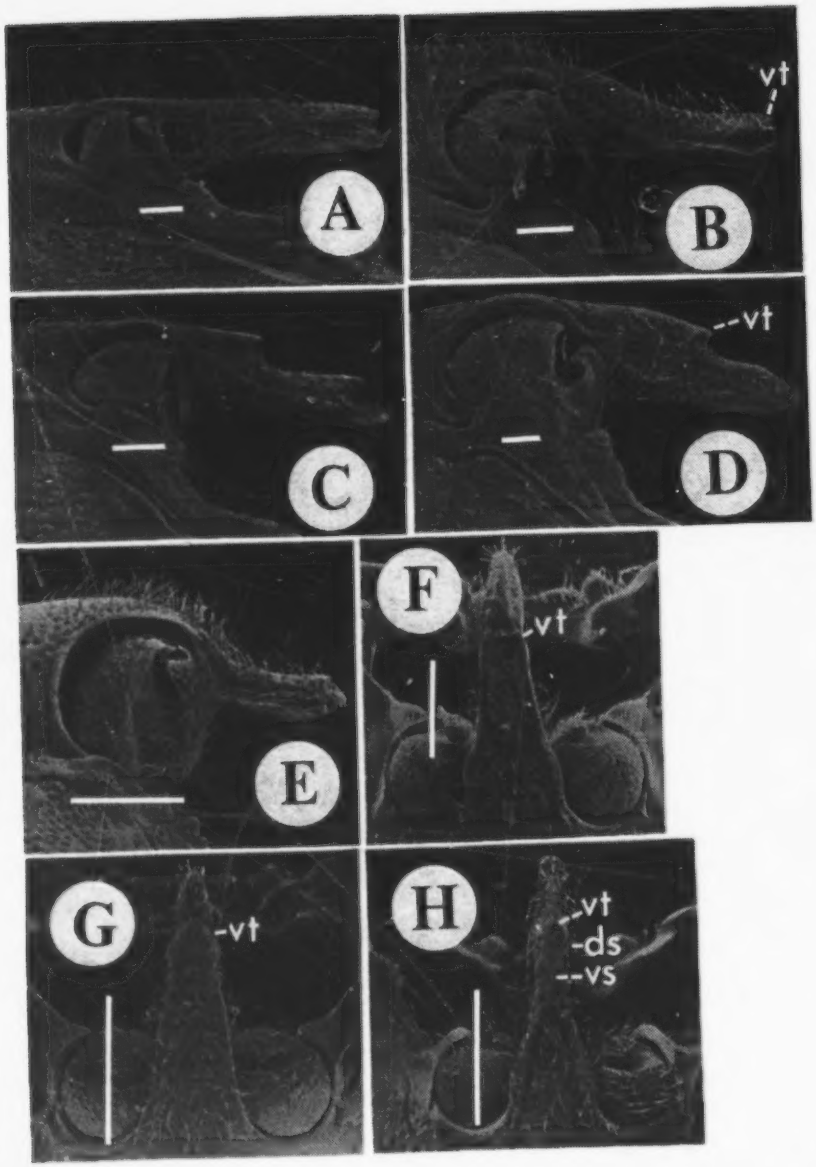

A
vt
B
--vt
C
D
F
-vt
E
G
-vt
H
--vt
-ds
--vs

Figure 7. Scanning electron micrographs of prothorax, mesosternum. A, B, proendosternite, posterior; A: Dalopius marginatus; B: Agriotes sp. C-H, mesosternum; C: Neotrichophorus carolinensis, ventrolateral; D: Dalopius marginatus, ventrolateral; E: Orthostethus infuscatus, lateral; F: Ctenoplus brunneus, ventrolateral; G: Adrastus sp., lateral; H: Parallelostethus attenuatus, ventrolateral. m - prosternal mucro, pe - proendosternite. Scale bar, A,B,D = 200 μm, C,E-H = 400 μm.

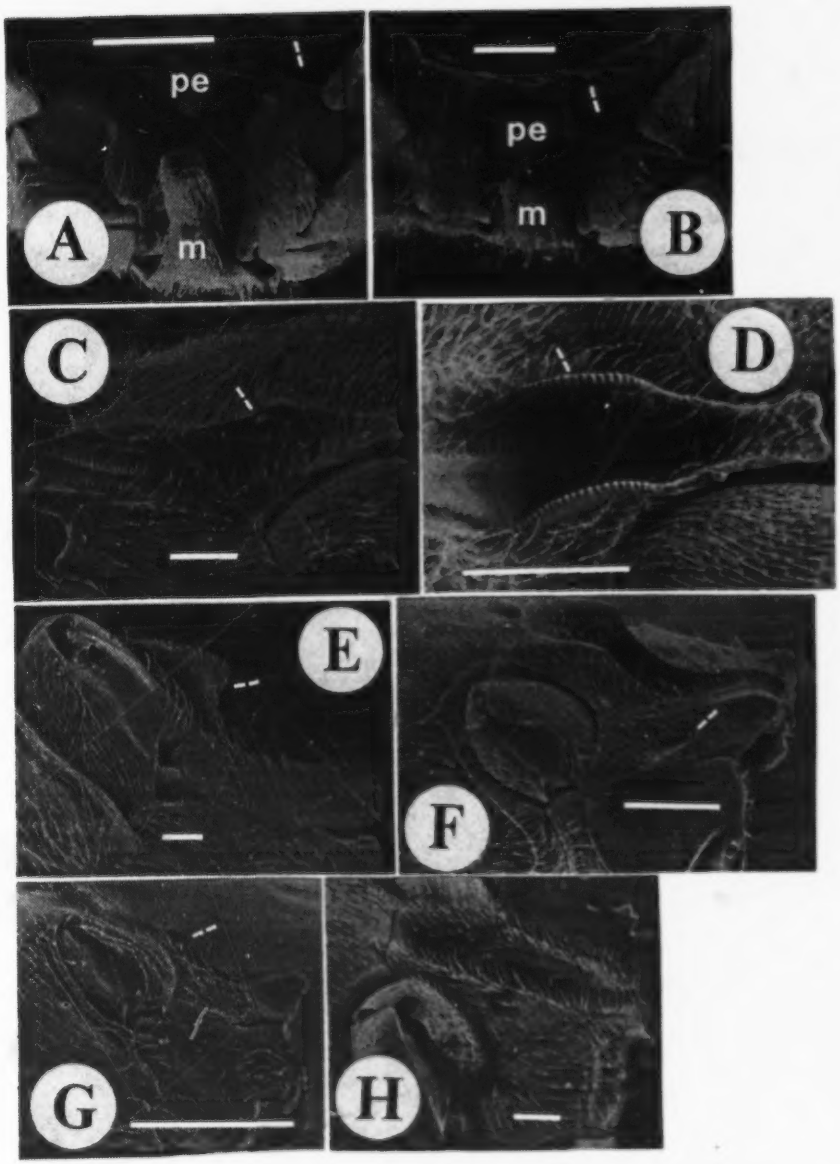

pe
A
m
pe
m
B
C
D
E
F
G
H

Figure 8. Scanning electron micrographs of ventral mesothoracic structures. A-F, mesothorax, ventral; A: Glyphonyx sp.; B: Neotrichophorus guillebeaui; C: Neotrichophorus carolinensis; D: Dalopius marginatus; E: Aphanobius sp.; F: Parallelostethus attenuatus. G,H, mesepimeron and mesepisternum, ventrolateral; G: Neotrichophorus carolinensis; H: Atractopterus honestus. ar - anterior articulating surface; g - Y-shaped groove, mt - mesotrochantin. Scale bar, A,F = 200 μm, B-E,G,H = 400 μm.

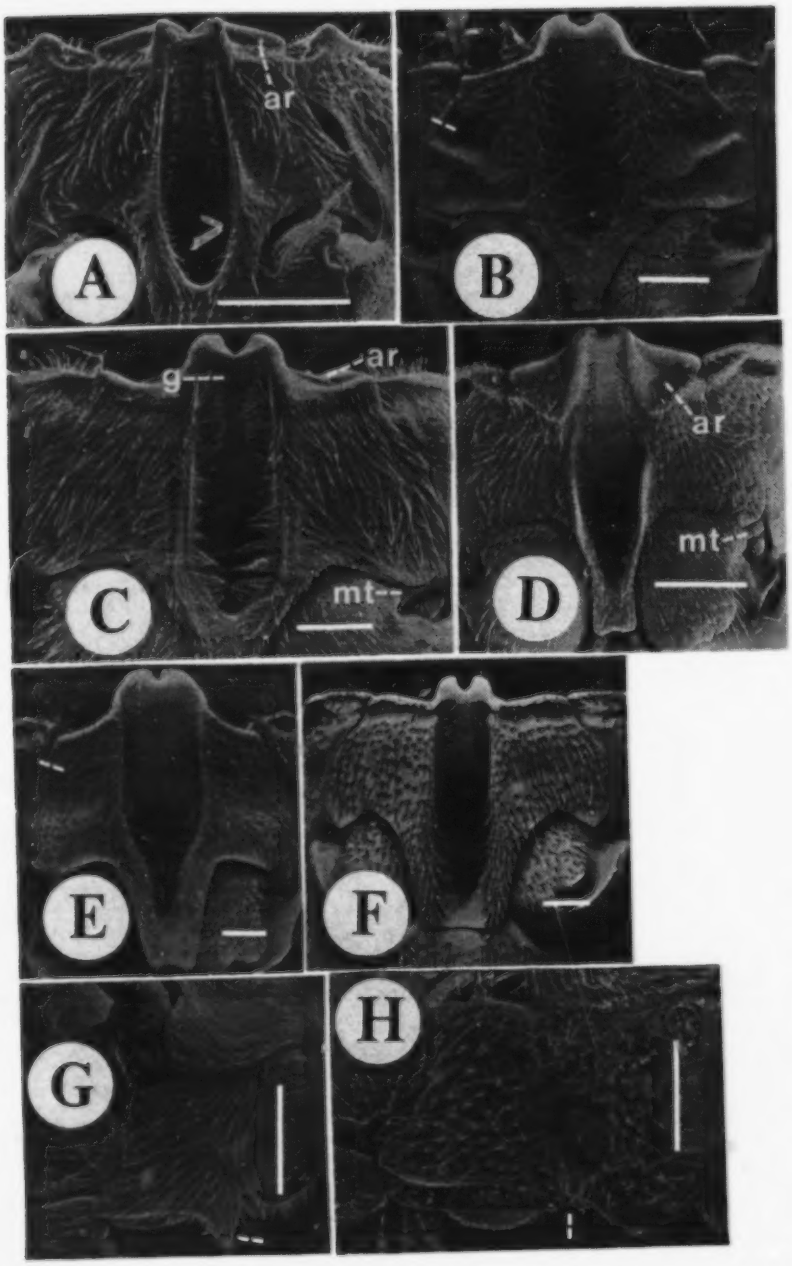

ar
A
B
g
ar
C
mt
ar
mt
D
E
F
G
H

Figure 9. Scanning electron micrographs of meso- and metathoracic structures. A-C, meso-metasternum, ventral; A: Neotrichophorus carolinensis; B: Parasilesis musculus; C: Glyphonyx sp. D, mesosternum, ventrolateral, Dalopius marginatus. E, metasternum, ventrolateral, Deromecus vulgaris. F,G, metacoxal plate, ventrolateral; F: Orthostethus infuscatus; G: Neotrichophorus carolinensis. ar - anterior articulating surface of mesosternum, f - mesosternal fossa, l - lateral lobe of mesosternum, m - metasternum, ms - mesepisternum, mp - mesepimeron. Scale bar, A,E,F,G = 1 mm, B-D, = 400 μm.

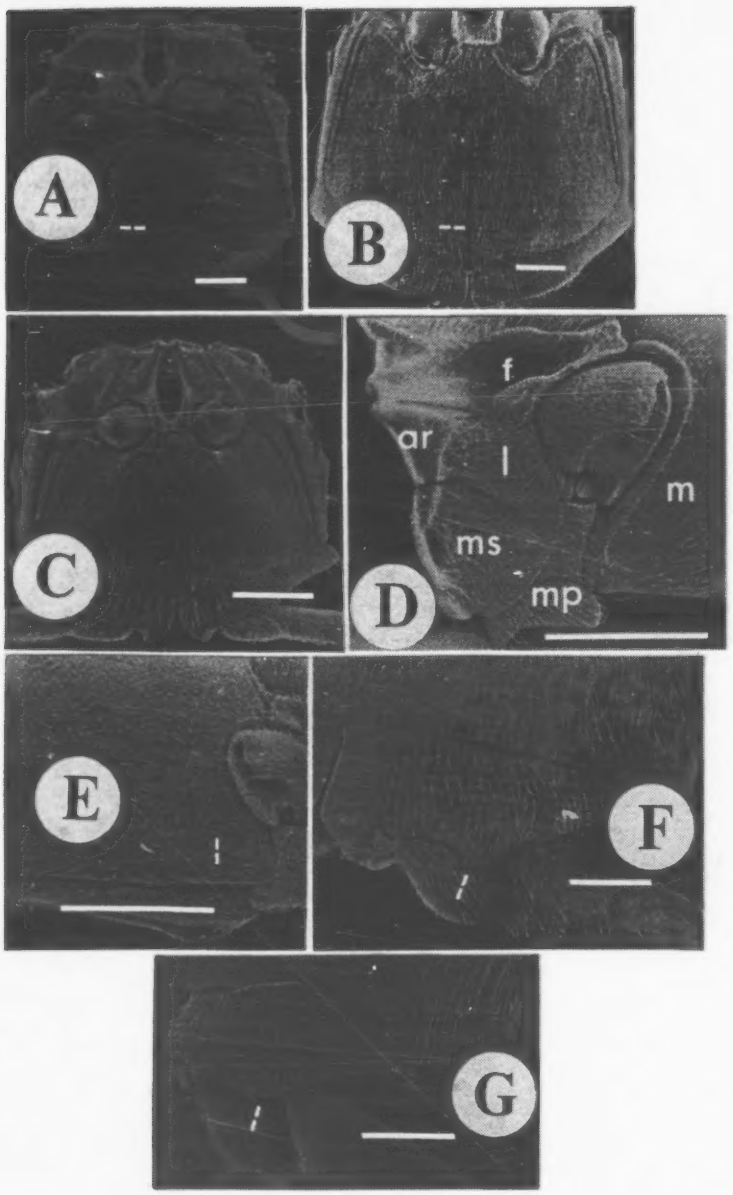

A
B
C
D
f
ar
l
m
ms
mp
E
F
G

Figure 10. Scanning electron micrographs of tarsi, photographs of female genital structures. A-F, tarsus; A: Dalopius marginatus, lateral; B: Pomachilius linearis, lateral; C,D: Glyphonyx sp., lateral; E: Pomachilius linearis, dorsal; F: Ypsilostethus semiotulus, tarsal claw; G: Synaptus filiformis, tarsal claw. H-J, ovipositor; H: Agriotes (Ectinus) aterrimus, dorsal; I: Parallelostethus attenuatus, ventral; J: Elater ferrugineus, ventral. K, abdominal segment VIII, ventral, Parallelostethus attenuatus. B - basal part of gonocoxite, P - apical part of gonocoxites, ss - posterior margin of spiracular sclerite, st - stylus of gonocoxites, su - ventral suture, vf - baculi, VIIIa - apodemes of segment VIII, VIIIs - sternum VIII Xt - tergum X. Scale bar, A-G = 100 μm, H-K = 0.5 mm.

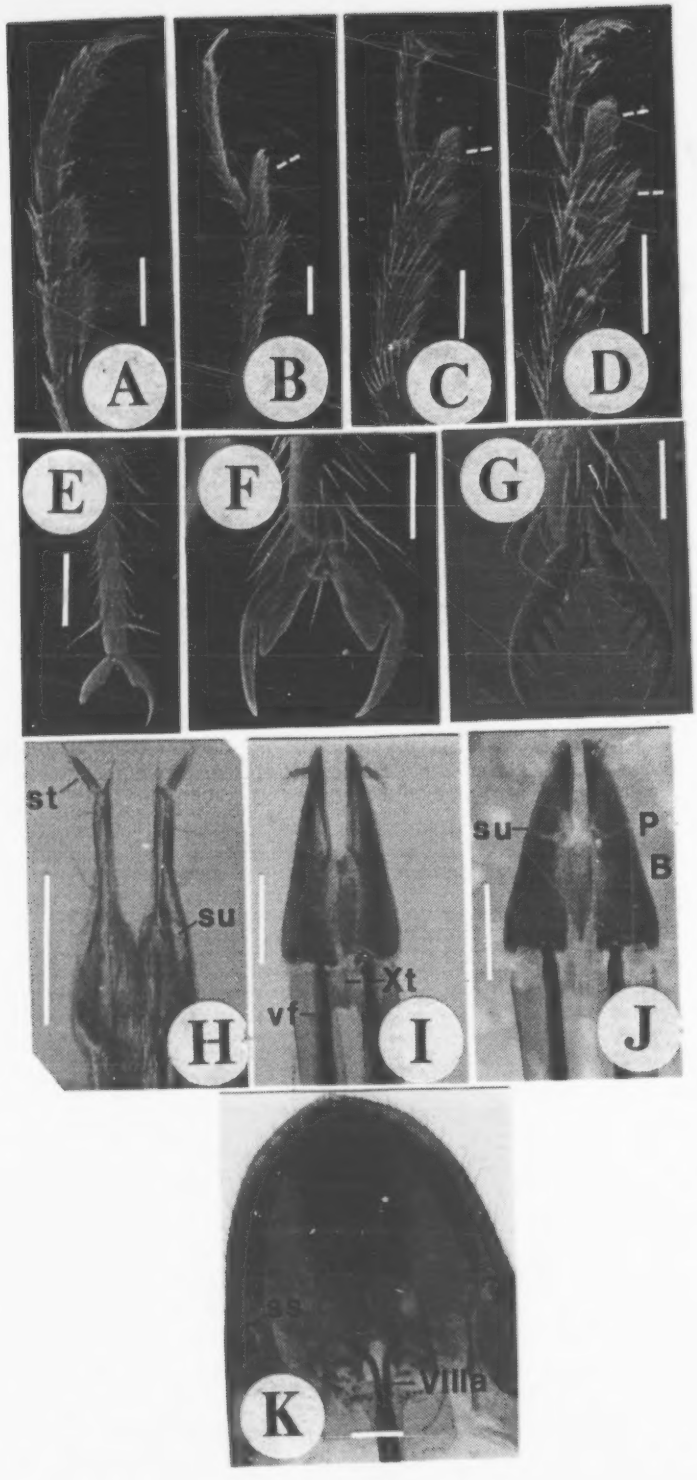

A
B
C
D
E
F
G
st
su
H
Xt
vf
I
su
P
B
J
ss
VIIIa
K

Figure 11. Photomicrographs of bursa copulatrices. A: Neotrichophorus guillebeaui; B: Neotrichophorus carolinensis; C: Parallelostethus attenuatus; D: Elater ferrugineus; E: Ypsilostethus semiotulus; F: Agriotes (Ectinus) aterrimus; G: Glyphonyx inquinatus; H: Dalopius cognatus. ag - accessory gland, bp - spiny plates of bursa, bs - bursal spines, cg - colleterial glands, sd - spermathecal duct. Scale bar = 0.5 mm.

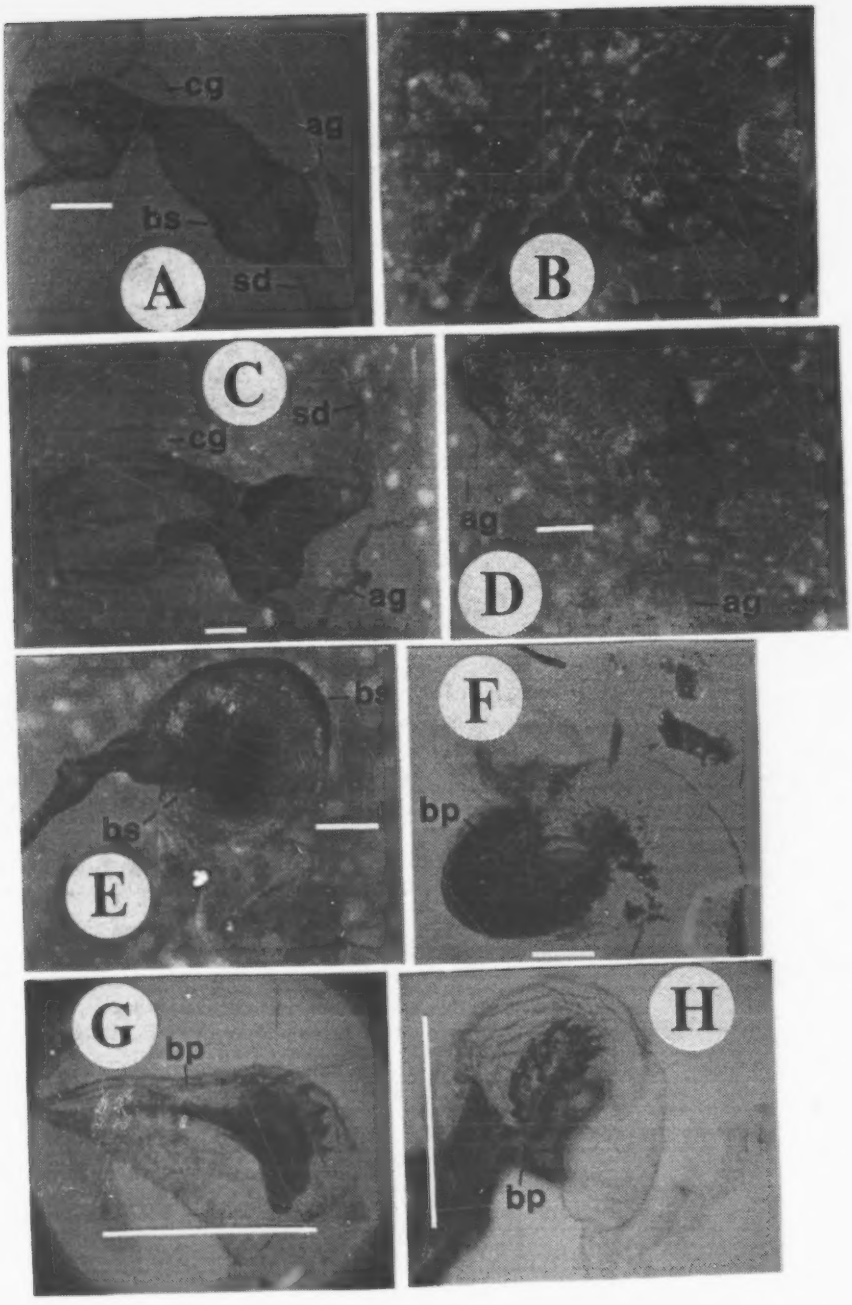

cg
ag
bs
A
sd
B
C
sd
cg
ag
ag
D
ag
bs
bs
E
F
bp
G
bp
H
bp

Figure 12. Hypothesized reconstructed phylogeny of the Elaterini. Letters in boxes identify hypothetical ancestors. Numbers indicate appearance of a change in state of the character corresponding to that number in the text. Numbers in square brackets indicate potential change of state. 'H' and 'R' represent independent evolution of an apomorphic state and reversal to a previous state respectively. See text for explanation of character states.

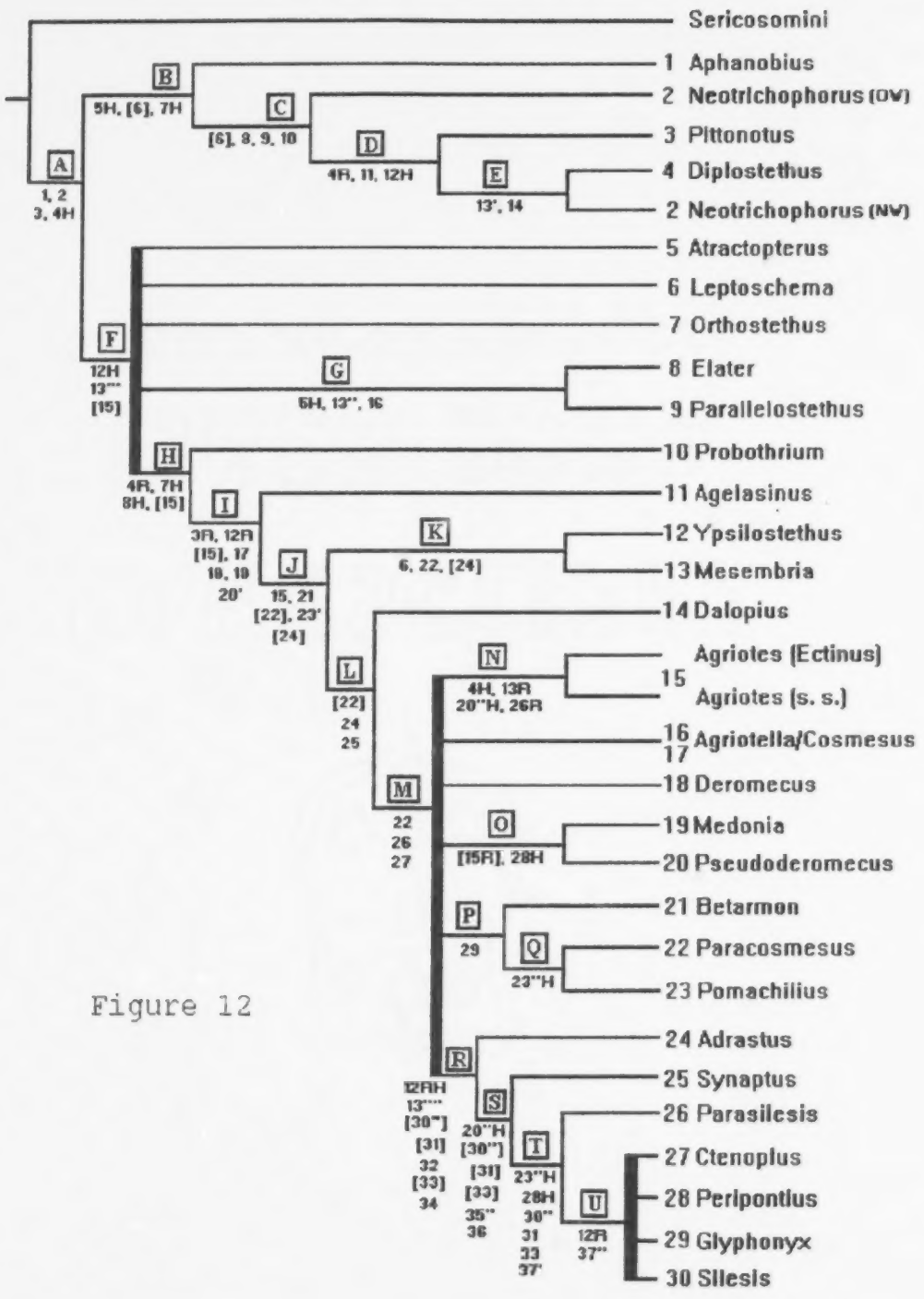

Sericosomini
1 Aphanobius
2 Neotrichophorus (OV)
3 Pittonotus
4 Diplostethus
2 Neotrichophorus (NV)
5 Atractopterus
6 Leptoschema
7 Orthostethus
8 Elater
9 Parallelostethus
10 Probothrium
11 Agelasinus
12 Ypsilostethus
13 Mesembria
14 Dalopius
15
Agriotes (Ectinus)
Agriotes (s. s.)
16
17
Agriotella/Cosmesus
18 Deromecus
19 Medonia
20 Pseudoderomecus
21 Betarmon
22 Paracosmesus
23 Pomachilius
24 Adrastus
25 Synaptus
26 Parasilesis
27 Ctenoplus
28 Peripontius
29 Glyphonyx
30 Sllesis
A
1, 2
3, 4H
B
5H, [6], 7H
C
[6], 8, 9, 10
D
4R, 11, 12H
E
13', 14
F
12H
13'''
[15]
G
5H, 13'', 16
H
4R, 7H
8H, [15]
I
3R, 12R
[15], 17
18, 19
20'
J
15, 21
[22], 23'
[24]
K
6, 22, [24]
L
[22]
24
25
M
22
26
27
N
4H, 13R
20''H, 26R
O
[15R], 28H
P
29
Q
23''H
R
12RH
13'''
[30'']
[31]
32
[33]
34
S
20''H
[30'']
[31]
[33]
35''
36
T
23''H
28H
30''
31
33
37'
U
12R
37''

Figure 12

Figures 13-15. Possible resolutions of polychotomies in Fig. 12. Figs. 13, 14: possible resolutions of polychotomy arising from Ancestor F. Fig. 15: one possible resolution of polychotomy arising from Ancestor M; see also Figs. 16, 17. Numbers and symbols as in Fig. 12. See text for explanation of character states.

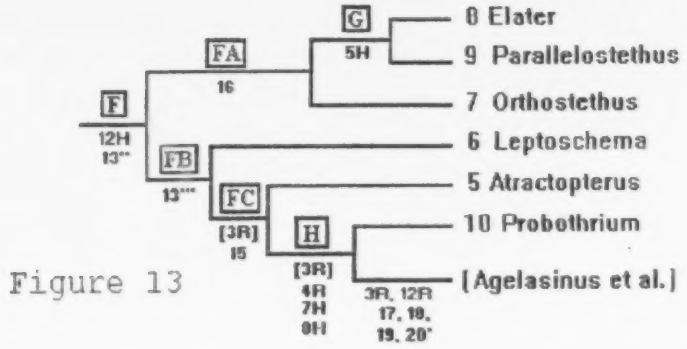


Figure 13

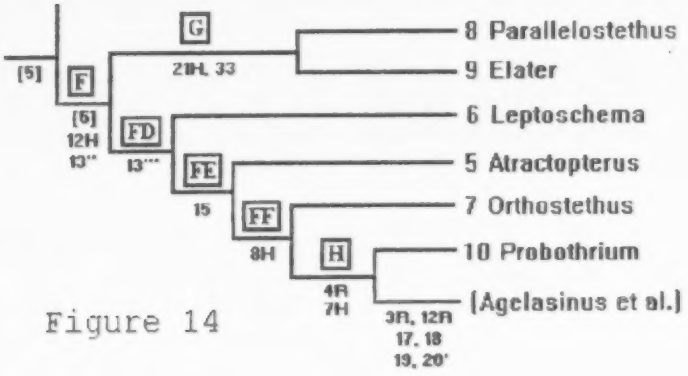
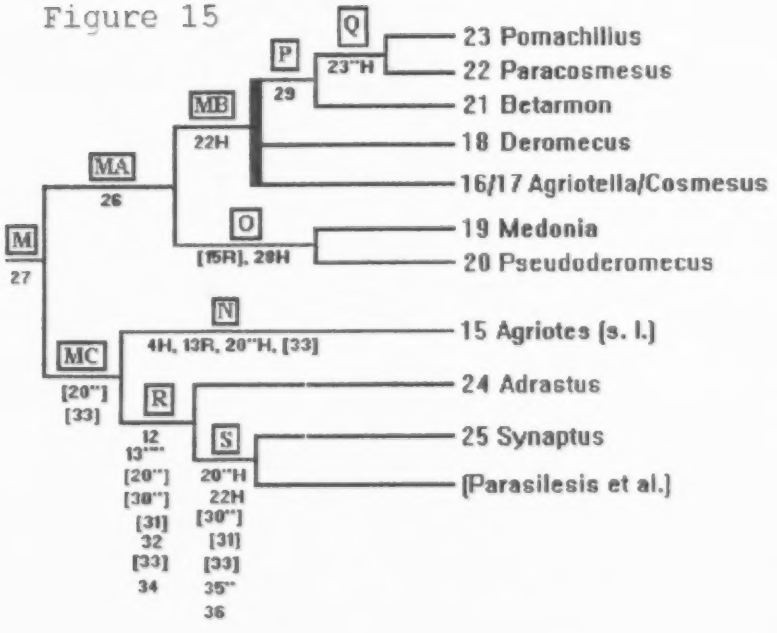


Figure 14

Figure 15



Figures 16-19. Possible resolutions of polychotomies in Fig. 12. Figs. 16, 17: possible resolutions of polychotomy arising from Ancestor M; see also Fig. 15. Figs. 18, 19: possible resolutions of polychotomy arising from Ancestor U. Numbers and symbols as in Fig. 12. See text for explanation of character states.

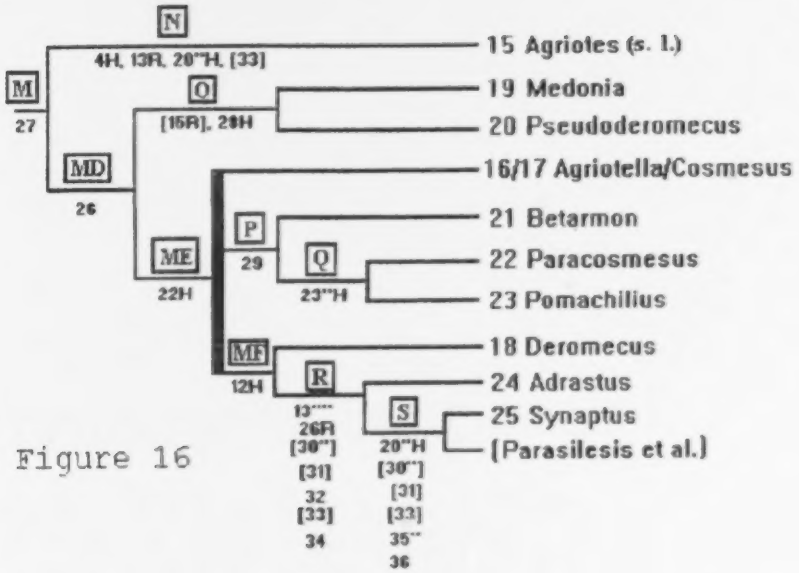


Figure 16

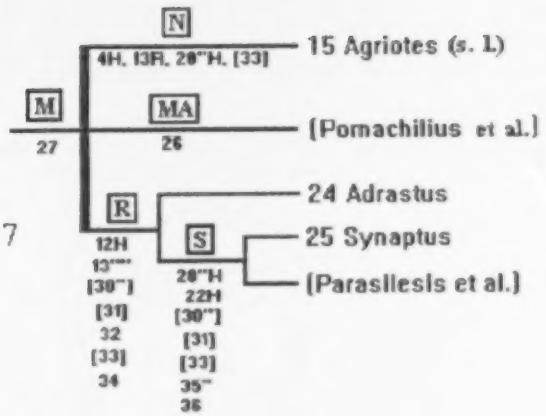


Figure 17

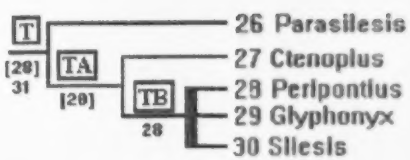


Figure 18

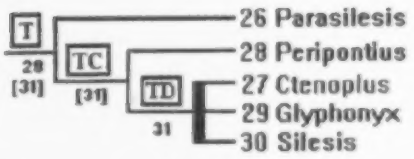


Figure 19

Figure 20. Hypothesized reconstruction of land mass configurations in Late Cretaceous Period, showing probable dispersal route of Ancestor H from West Euramerica into South America. Map from Briggs (1987, Map 5).

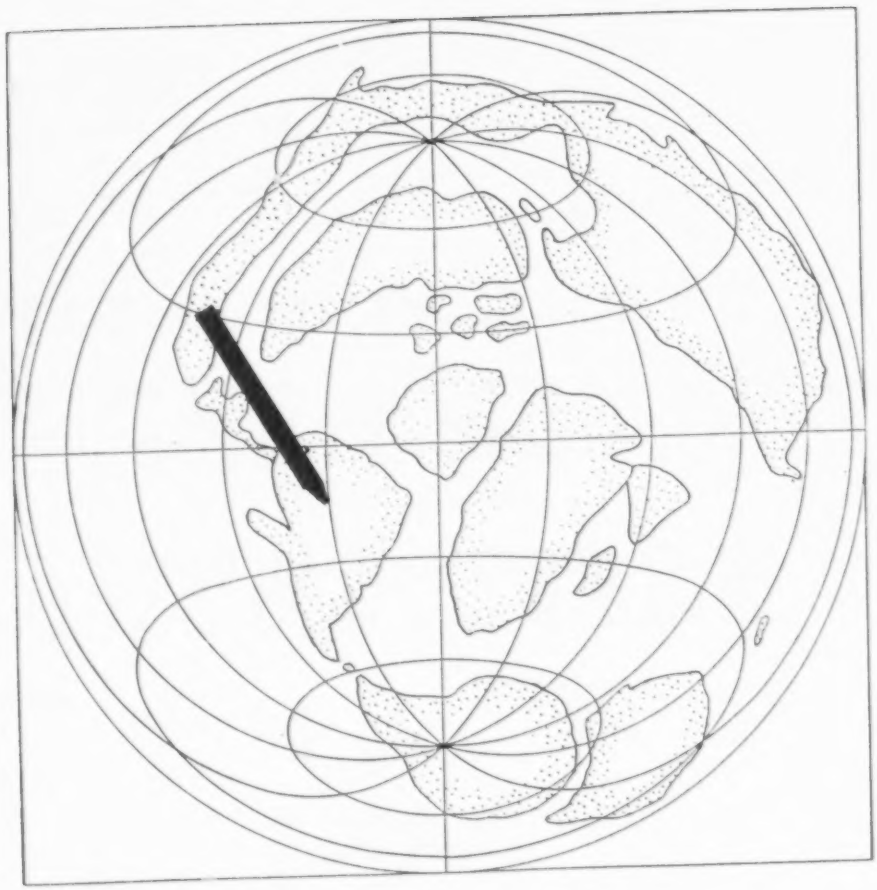
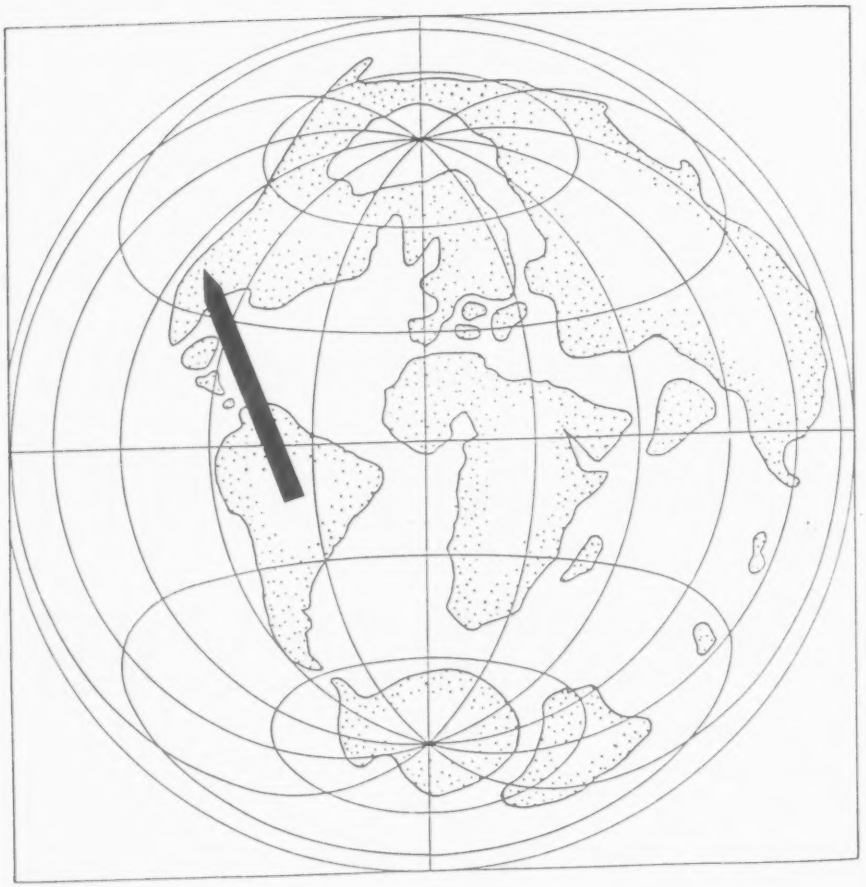



Figure 21. Hypothesized reconstruction of land mass configurations in Paleocene Epoch, showing probable dispersal route from South America into Euramerica of Ancestors N and R, or Ancestor MC. See text for details. Map from Briggs (1987, Map 6).